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# *GOCHNATIA* (ASTERACEAE, MUTISIEAE) AND THE *GOCHNATIA* COMPLEX: TAXONOMIC IMPLICATIONS FROM MORPHOLOGY<sup>1</sup>

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## ABSTRACT

*Gochnacia* is one of the largest genera of the tribe Mutisieae (Asteraceae) and has been traditionally characterized by its homogamous capitula with isomorphic corollas. A morphological study of *Gochnacia* and associated genera, i.e., *Actinoseris*, *Chuoa*, *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, *Pleiotaxis*, and *Wunderlichia*, was carried out to evaluate the circumscription of *Gochnacia* and its sections, and the affinities of this complex of genera. The characters studied involve habit, leaf features (consistency, pubescence type, shape, margin, and venation), types of capitulescence, involucre features (shape, size, phyllary series, pubescence, and shape), paleae, floret features (morphology, sex, number, color of corolla, anthers, style shapes, achenial pubescence, and pappus). Analysis of these features revealed: (1) although *Gochnacia* is highly variable in most of the characters studied, it can be defined by this suite of features: isomorphic to subdimorphic corollas, apiculate anther appendages, and smooth style branches; (2) sections of *Gochnacia* needed to be re-evaluated. As result of this, two sections, i.e., sect. *Discoseris* and sect. *Pentaphorus*, are confirmed; two sections are proposed, i.e., sect. *Glomerata* sect. nov. and sect. *Rotundifolia* sect. nov.; three sections are redefined, i.e., sect. *Hedraiophyllum*, sect. *Leucomeris*, and sect. *Gochnacia*, while sect. *Anastraphioides* is formally published; and (3) the combination of apiculate anther appendages and smooth style branches is unique to *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnacia*, *Hyalis*, *Ianthopappus*, and *Nouelia* within the Mutisieae. This group of genera is recognized here as the *Gochnacia* complex, with *Gochnacia* as the basal genus of this complex. *Chuoa*, *Pleiotaxis*, and *Wunderlichia* do not belong to the *Gochnacia* complex.

**Key words:** Asteraceae, Compositae, *Gochnacia*, *Gochnacia* complex, infrageneric classification, morphology, Mutisieae.

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*Gochnacia* Kunth is one of the largest genera of the tribe Mutisieae, subtribe Mutisiinae sensu lato (including Gochnatiinae; Robinson, 1991; Bremer, 1994). It comprises 68 species, nearly all Neotropical and 2 endemic to the mountains of southeastern Asia. All the species of *Gochnacia* have been traditionally described as discoid with actinomorphic, deeply 5-lobed corollas, features that are plesiomorphic within Mutisieae (Bremer, 1994). The only apomorphic character suggested for the genus is the acuminate to apiculate apical anther appendage of the stamens (Bremer, 1994). This character, however, is shared by other genera of Mutisieae.

The infrageneric taxonomy of *Gochnacia* has been much discussed (Lessing, 1832; de Candolle,

1838; Jervis, 1954; Cabrera, 1971) since the genus was established by Kunth (1818). Cabrera (1971), in his monograph of the genus, divided it into six sections: sect. *Discoseris*, sect. *Gochnacia*, sect. *Hedraiophyllum*, sect. *Leucomeris*, sect. *Moquinias-trum*, and sect. *Pentaphorus*. He suggested the artificial delimitation of some sections, such as *Hedraiophyllum*, and in other cases emphasized geographical distribution in distinguishing groups of species, such as in section *Gochnacia*.

Jeffrey (1967), when relating *Gochnacia* to other taxa, established the *Stiffia*-series of genera, which all have short, rounded, glabrous style arms, and commonly glabrous corollas. The *Stiffia*-series was then divided into four subseries by slight differences in the shape of the style arms, although these

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differences were not described for each subseries. Of these subseries, the *Gochnatia*-subseries included *Achnopogon*, *Cnicothamnus*, *Gochnatia*, *Nouelia*, and *Oldenburgia*.

Cabrera (1971) considered *Actinoseris*, *Cyclolepis*, and *Pleiotaxis* closely related to *Gochnatia* by their apiculate anthers. Later, he also associated *Chuoa* with *Gochnatia* (Cabrera, 1977). Hansen (1991) considered only *Actinoseris* and *Cyclolepis* of Cabrera's group to be close to *Gochnatia*, excluding *Pleiotaxis* and *Chuoa*, and added *Hyalis* and *Nouelia* to what he called the "Gochnatia-group." Hansen argued the presence of cone-like involucres, i.e., with light brownish bracts imbricately arranged and resembling the cone of a spruce as a probable synapomorphy of the group. Recently, Roque and Hind (2001) created the new genus *Ianthopappus* for the species *Actinoseris corymbosa*. In this work, the authors grouped the genera *Actinoseris*, *Chuoa*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, and *Nouelia* by their apiculate to acuminate apical anther appendages. Furthermore, Roque (2001) and Roque and Pirani (2001) re-circumscribed the genus *Richterago* Kunze according to the genus concept first employed by Lessing (1830) to include the species of *Actinoseris* and the species of *Gochnatia* sect. *Discoseris*. We consider, however, that the characters used to distinguish *Richterago* are widespread in *Gochnatia* or are shared with other genera, such as herbaceous to subshrubby habit (shared among *Gochnatia* sect. *Discoseris*, *Actinoseris*, and other such related genera as *Hyalis* and *Ianthopappus*), leaves rosulate to alternate (alternate leaves are present in most species of *Gochnatia*), venation pinnate (present in most species of *Gochnatia*), capitula homogamous and discoid (present in most species of *Gochnatia*) or heterogamous and radiate (present in some species of *Actinoseris*), as well as pappus features, i.e., pappus uniseriate, with 25 to 42 bristles, united into a fleshy ring (present in species of *Gochnatia* sect. *Gochnatia*). For these reasons, we affirm here the traditional concept of *Gochnatia* and *Actinoseris* (excluding *A. corymbosa* = *Ianthopappus corymbosus*) as was established by Cabrera (1970, 1971).

Some phylogenetic studies relate *Gochnatia* with other genera of Mutisieae; for example, Jansen and Palmer (1987) related *Gochnatia* with *Ainsliaea*, *Onoseris*, and *Stiftia*, and Karis et al. (2001) related it with *Mutisia* and *Trixis*. However, because of the few taxa sampled in the tribe, these analyses are not considered here to address relationships at the generic level.

In other analyses (Karis et al., 1992; Jansen &

Kim, 1996), *Gochnatia* was found to be an isolated taxon within Cichorioideae. The cladogram of Karis et al. (1992), based on morphological characters, shows *Gochnatia* as sister to most Asteraceae, excluding Barnadesioideae and four genera of Gochnatiinae. The *ndhF* tree of Jansen and Kim (1996) also shows *Gochnatia* as an independent lineage positioned basal to most Asteraceae, excluding Barnadesioideae and the core of Mutisieae examined. There are other genera within Mutisieae such as *Quelchia* and *Neblinaea* from the Guayana Highland with apiculate anther appendages, but morphological features of these genera (Pruski, 1991; Bremer, 1994) mark a departure from *Gochnatia* and associated taxa. On the other hand, the planaltive Brazilian genus *Wunderlichia*, with shortly apiculate anther appendages, was either placed in the "Stenopadus group" (Pruski, 1991) or it was considered isolated within Mutisieae (Hansen, 1991; Karis et al., 1992; Bremer, 1994).

The group selected here for the analysis is mainly represented by the genera with apiculate anther appendages suggested by Jeffrey (in part, 1967), Cabrera (1971, 1977), Hansen (1991), and Roque and Hind (2001). It is comprised of *Actinoseris* sensu Cabrera, excluding *A. corymbosa* (7 species), *Chuoa* (1 species), *Cnicothamnus* (2 species), *Cyclolepis* (1 species), *Gochnatia* (68 species), *Hyalis* (2 species), *Ianthopappus* (1 species), *Nouelia* (1 species), *Pleiotaxis* (ca. 25 species), and the controversial *Wunderlichia* (6 species).

There are several potential diagnostic features in *Gochnatia* and relatives such as the habit, leaf morphology, types of capitulecence, involucre, florets, trichomes, and pappus that have never been studied comparatively or in detail. A detailed morphological study of *Gochnatia* and its associated taxa is needed as a first step to provide a robust base for discussion.

On the basis of morphological evidence, the goals of this study are: (1) to evaluate the circumscription of *Gochnatia* and its sections, and (2) to group *Gochnatia* with other genera based on their similarities.

## MATERIAL AND METHODS

Herbarium specimens of the studied taxa, i.e., *Actinoseris*, *Chuoa*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia* (64 of its 68 species), *Hyalis*, *Ianthopappus*, *Nouelia*, *Pleiotaxis*, and *Wunderlichia* (Appendix 1), were examined to assess characters used previously to distinguish taxa in this group of genera, and to search for additional characters. The data were augmented by literature studies (Fran-

chet, 1888; Cabrera, 1950, 1951, 1955, 1970, 1971; Jeffrey, 1967; Barroso & Maguire, 1973; Zardini, 1975; Sancho, 1997, 2000; Roque, 1997; Roque & Hind, 2001; Roque & Pirani, 1997, 2001).

Vegetative and floral parts were dissected and observed after boiling in water and stained with 2% safranin. Freehand sections of leaves were performed and these sections examined to determine the presence of hypodermis, and then stained with safranin. Drawings were made by the authors using a stereomicroscope Wild M5 and a microscope Leitz SM Lux with the camera lucida technique.

Apical anther appendages were described and drawn to include the portion ranging from the thecae apex to the apex of the stamen.

Descriptive terminology for the trichomes follows Ramayya (1962). Whenever possible, additional synonyms of trichome terminology were added (Payne, 1978; Font Quer, 1979; Moreno, 1984; Harris & Harris, 1994; Metcalfe & Chalk, 1950). Some authors use the term "trichome," whereas others apply the term "hair" in their pubescence classifications. Both terms are cited here following each author classification.

## RESULTS

For comparison with our results, sections of *Gochnatia* with their corresponding species according to Cabrera (1971) are listed in Table 1.

### VEGETATIVE CHARACTERS

**Habit.** Taxa under study display four types of habit: small trees, shrubs, subshrubs, and perennial herbs. Several species of *Gochnatia* (e.g., *G. arborescens*, *G. decora*, *G. elliptica*, *G. ilicifolia*, *G. magna*, *G. oligocephala*, *G. palosanto*, *G. polymorpha*, *G. spectabilis*, *G. tortuensis*), *Cnicothamnus*, and *Wunderlichia* are small trees. Most species of *Gochnatia*, *Chuoa*, *Cyclolepis*, and *Nouelia* are shrubs. *Gochnatia* sect. *Discoseris*, *Hyalis*, and *Ianthopappus* are subshrubs. *Actinoseris* and *Pleiotaxis* are perennial herbs. *Cyclolepis* is the only spinose genus and is aphyllous at maturity.

**Leaves.** All taxa analyzed have alternate, occasionally rosulate, subsessile to shortly petiolate leaves.

**Leaf consistency:** The leaves are coriaceous or subcoriaceous, but only some species have leaves with an adaxial hypodermis. It is absent in some species of *Gochnatia* (e.g., *G. amplexifolia*, *G. arequipensis*, *G. cardenasii*, *G. discoidea*, *G. foliolosa*, *G. glutinosa*, *G. hypoleuca*, *G. intertexta*, *G. magna*,

*G. palosanto*, *G. purpusii*, *G. rotundifolia*, *G. vernonioides*), *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, and in some species of *Pleiotaxis* (e.g., *P. eximia*, *P. huillensis*). Occasionally, the hypodermis is discontinuous (e.g., *Gochnatia argentina*, *G. discolor*, *G. orbiculata*, *G. ramboi*).

**Leaf shape:** The leaves are always simple in the taxa under study, but show great variation in shape, from linear to suborbicular. Most species of *Gochnatia* sect. *Gochnatia* and *Nouelia* have leaves ovate to ovate-elliptic, obtuse to subobtuse at the apex; occasionally ovate leaves are acute at the apex (e.g., *G. polymorpha*, *G. vernonioides*), or cordate at the base (e.g., *G. cordata*, *G. haumaniana*) (Fig. 1A). Most of the Caribbean species of *Gochnatia* sect. *Gochnatia*, *Actinoseris* (*A. hatschbachii*, *A. polymorpha*, *A. radiata*), *Chuoa*, *Ianthopappus*, and *Wunderlichia* have obovate leaves (Fig. 1B). Elliptic leaves (Fig. 1C) are rounded in the base and apex in *G. discoidea*, attenuate at the base and apex in *G. magna*, *G. sect. Leucomeris*, *Actinoseris* (*A. polyphylla*), *Cnicothamnus*, and some species of *Pleiotaxis* (e.g., *P. huillensis*, *P. newtonii*, *P. selina*, *P. subscaposa*). *Gochnatia* sect. *Pentaphorus*, *G. argyrea*, *Actinoseris* (*A. angustifolia*, *A. stenophylla*), *Cyclolepis*, *Hyalis*, and most species of *Pleiotaxis* (e.g., *P. ambigua*, *P. decipiens*, *P. dewevrei*, *P. linearifolia*, *P. rogersii*) have linear leaves (Fig. 1D).

**Leaf margin:** Only the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. crassifolia* and *G. picardae*) and *Chuoa* have spinose margins (Fig. 1E). In the remaining taxa the leaf margin is predominantly entire or denticulate (Fig. 1F).

**Leaf venation:** The venation is predominantly pinnate, although in taxa such as *Gochnatia arequipensis*, *G. glutinosa*, *G. rotundifolia*, *Hyalis*, and *Ianthopappus* the leaves are three-veined (actinodromous).

### CAPITULESCENCE

Capitula are borne singly or 2 or 3 at the end of the branches or may be clustered in pseudocorymbs, pseudoracemes, or pseudopanicles, in open to condensed or glomerulose synflorescences depending upon the length of the peduncles.

Solitary or few capitula (2 or 3) are short-pedunculate to glomerulose in *Gochnatia* sect. *Gochnatia*, *Cnicothamnus*, *Nouelia*, and some species of *Wunderlichia* (*W. azulensis*, *W. crulsiana*, *W. mirabilis*) (Fig. 2A). They are scapiform, long-pedunculate in *Gochnatia suffrutescens*, some species of *Actinoseris* (e.g., *A. angustifolia*, *A. hatschbachii*, *A. polymorpha*, *A. radiata*), *Chuoa*, and some species of *Pleiotaxis* (e.g., *P. subscaposa*) (Fig. 2B).

Table 1. Sections within *Gochnertia* established in this study on the basis of the morphology, compared with the sections delimited by Cabrera (1971), with the addition of *G. hatschbachii* (Cabrera, 1974) and *G. densiephala* (Sancho, 2000). The geographic distribution and diagnostic characters for each section are provided, with uncommon features appearing in parentheses. \* = type species of each section.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
<i>Gochnertia</i> sect. <i>Discoseris</i>	<i>Gochnertia</i> sect. <i>Discoseris</i>		Subshrubs; capitula solitary, long-pedunculate, or numerous in scapose pseudocorymbs; appendage abruptly apiculate, laciniate tails; pappus type A
<i>G. amplexifolia</i> (Gardner) Cabrera	<i>G. amplexifolia</i>	Brazil	
* <i>G. discoidea</i> (Less.) Cabrera	<i>G. discoidea</i>	Brazil	
<i>G. suffrutescens</i> Cabrera	<i>G. suffrutescens</i>	Brazil	
<i>Gochnertia</i> sect. <i>Gochnertia</i>	<i>Gochnertia</i> sect. <i>Gochnertia</i>		
South American species:			
<i>G. arequipensis</i> Sandw.	<i>G. arequipensis</i>	Peru	
<i>G. boliviiana</i> S. F. Blake	<i>G. boliviiana</i>	Bolivia	
<i>G. cardenasi</i>	<i>G. cardenasi</i>	Bolivia	
<i>G. curviflora</i> (Griseb.) O. Hoffm.	<i>G. curviflora</i>	S Bolivia, NW Argentina	
<i>G. patazina</i> Cabrera	<i>G. patazina</i>	Peru	
<i>G. vargasii</i> Cabrera	<i>G. vargasii</i>	Peru	
* <i>G. vernonioides</i> Kunth	<i>G. vernonioides</i>	N Peru	
<i>Gochnertia</i> sect. <i>Rotundifolia</i>	<i>Gochnertia</i> sect. <i>Rotundifolia</i>	S Brazil	
<i>G. rotundifolia</i> Less.	* <i>G. rotundifolia</i>		
Caribbean species:			
<i>G. attenuata</i> (Britton) Jervis & Alain	<i>G. attenuata</i>	Cuba	
<i>G. buchii</i> (Urb.) Jiménez	<i>G. buchii</i>	Caribbean	
<i>G. calcicola</i> (Britton) Jervis & Alain	<i>G. calcicola</i>	Cuba	
<i>G. couellii</i> (Britton) Jervis & Alain	<i>G. couellii</i>	Cuba	
<i>G. crassifolia</i> (Britton) Jervis & Alain	<i>G. crassifolia</i>	Cuba	
<i>G. cubensis</i> (Carabia) Jervis & Alain	<i>G. cubensis</i>	Cuba	
<i>G. ekmanii</i> (Urb.) Jervis & Alain	<i>G. ekmanii</i>	Cuba	
<i>G. elliptica</i> (León) Alain	<i>G. elliptica</i>	Cuba	
<i>G. enneantha</i> (S. F. Blake) Alain	<i>G. enneantha</i>	Dominican Republic	
<i>G. gomezii</i> (León) Jervis & Alain	<i>G. gomezii</i>	Cuba	
* <i>G. ilicifolia</i> Less.	<i>G. ilicifolia</i>	Caribbean	

Table 1. Continued.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
<i>G. intertexta</i> (Griseb.) Jervis & Alain	<i>G. intertexta</i>	Cuba	
<i>G. maisiana</i> (León) Jervis & Alain	<i>G. maisiana</i>	Cuba	
<i>G. mantuensis</i> (Griseb.) Jervis & Alain	<i>G. mantuensis</i>	Cuba	
<i>G. microcephala</i> (Griseb.) Jervis & Alain	<i>G. microcephala</i>	Cuba	
<i>G. montana</i> (Britton) Jervis & Alain	<i>G. montana</i>	Cuba	
<i>G. obtusifolia</i> (Britton) Jervis & Alain	<i>G. obtusifolia</i>	Cuba	
<i>G. oligantha</i> (Urb.) Howard	<i>G. oligantha</i>	Caribbean	
<i>G. parvifolia</i> (Britton) Jervis & Alain	<i>G. parvifolia</i>	Cuba	
<i>G. pauciflosculosa</i> (Hitchc.) Cabrera	<i>G. pauciflosculosa</i>	Bahamas	
<i>G. picardae</i> (Urb.) Jiménez	<i>G. picardae</i>	Haiti	
<i>G. recurva</i> (Britton) Jervis & Alain	<i>G. recurva</i>	Cuba	
<i>G. sagittana</i> Jervis & Alain	<i>G. sagittana</i>	Cuba	
<i>G. shafieri</i> (Britton) Jervis & Alain	<i>G. shafieri</i>	Cuba	
<i>G. tortuensis</i> (Urb.) Jiménez	<i>G. tortuensis</i>	Haiti	
<i>G. wilsonii</i> (Britton) Jervis & Alain	<i>G. wilsonii</i>	Cuba	
<i>Gochnertia</i> sect. <i>Hedraiphyllum</i>	<i>Gochnertia</i> sect. <i>Glomerata</i>		
<i>G. arborescens</i> T. S. Brandegee	* <i>G. arborescens</i> (moved to another section)	Mexico	
* <i>G. cordata</i> Less.			
<i>G. magna</i> Cabrera	<i>G. magna</i>	Mexico	
<i>G. purpusii</i> T. S. Brandegee	<i>G. purpusii</i>	Mexico	
	<i>Gochnertia</i> sect. <i>Leucomeris</i>		
<i>G. hypoleuca</i> (DC.) A. Gray	<i>G. hypoleuca</i>	S U.S.A., Mexico	
<i>G. palosanto</i> Cabrera	<i>G. palosanto</i>	N Argentina, S Bolivia	
<i>G. smithii</i> Robinson & Greenm.	<i>G. smithii</i>	Mexico	
		Numerous capitula in glomerulose pseudocorymbs, pseudoracemes or pseudopanicles; involucre with glabrous, ciliolate at the margin phyllaries extending into the peduncle; florets 4 to 6(8 to 12), white (yellow); anther appendage attenuate (abruptly apiculate), laciniate tails (smooth); pap- pus type B	

Table 1. Continued.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
<i>Gochnia</i> sect. <i>Leucomeris</i>			
<i>G. decora</i> (Kurz) Cabrera	<i>G. decora</i>	Asia	
* <i>G. spectabilis</i> (D. Don) Less	<i>G. spectabilis</i>	Asia	
<i>Gochnia</i> sect. <i>Moquiniastrum</i>			
<i>G. argentina</i> (Cabrera) Cabrera	<i>G. argentina</i>	N Argentina	
<i>G. argyrea</i> (Malme) Cabrera	<i>G. argyrea</i>	S Brazil	
<i>G. barrosoii</i> Cabrera	<i>G. barrosoii</i>	S Brazil, Paraguay	
<i>G. blanchetiana</i> (DC.) Cabrera	<i>G. blanchetiana</i>	E Brazil	
	* <i>G. cordata</i> Less.	Paraguay, Brazil, Uruguay, Argentina	
	<i>G. densicephala</i> (Cabrera) G. Sancho	E Brazil	
<i>G. discolor</i> Baker	<i>G. discolor</i>	Brazil	
<i>G. floribunda</i> Cabrera	<i>G. floribunda</i>	Brazil	
<i>G. gardneri</i> (Baker) Cabrera	<i>G. gardneri</i>	Brazil	
	<i>G. hatschbachii</i> Cabrera	Brazil	
<i>G. haumaniana</i> Cabrera	<i>G. haumaniana</i>	Paraguay, Brazil	
<i>G. mollissima</i> (Malme) Cabrera	<i>G. mollissima</i>	S Brazil	
<i>G. oligocephala</i> (Gardner) Cabrera	<i>G. oligocephala</i>	E Brazil	
<i>G. orbiculata</i> (Malme) Cabrera	<i>G. orbiculata</i>	E Brazil	
<i>G. paniculata</i> (Less.) Cabrera	<i>G. paniculata</i>	SE Brazil	
<i>G. polymorpha</i> (Less.) Cabrera	<i>G. polymorpha</i>	Brazil, Paraguay, Uruguay, Argentina	
<i>G. pulchra</i> Cabrera	<i>G. pulchra</i>	S Brazil, Paraguay	
<i>G. ramboi</i> Cabrera	<i>G. ramboi</i>	S Brazil	
<i>G. rusbyana</i> Cabrera	<i>G. rusbyana</i>	Andes of Peru, Bolivia	
<i>G. sordida</i> (Less.) Cabrera	<i>G. sordida</i>	S Brazil	
<i>G. velutina</i> (Bong.) Cabrera	<i>G. velutina</i>	S Brazil	
<i>Gochnia</i> sect. <i>Pentaphorus</i>			
	<i>Gochnia</i> sect. <i>Pentaphorus</i>	Central Chile	
* <i>G. foliolosa</i> (D. Don) Hook. & Arn.	<i>G. foliolosa</i>	W Argentina	
<i>G. glutinosa</i> (D. Don) Hook & Arn.	<i>G. glutinosa</i>		
		Linear leaves, pinnately, three-veined, glandulate;	
		numerous capitula in glomerulose, leafy pseudo-	
		racemes; florets 5 (3, 7, or 10 to 20), white or	
		lilac; anther appendage abruptly apiculate,	
		smooth, laciniate, smooth tails; pappus type D	




Figure 1. Leaf shape. —A. Ovate (left to right): *Gochnatia rotundifolia* (Handro 157, LP), *G. ramboi* (Rambo 50005, S), *G. vernonioides* (López & Sagástegui 3354, LP), *G. cordata* (Serrano 6, LP), *Nouelia insignis* (l'Abbé Delavay 2498, US). —B. Obovate (left to right): *Wunderlichia crulsiana* (Ratter et al. 2615, MO), *Gochnatia intertexta* (Alain A-1680, NY), *G. pauciflosculosa* (Wilson 7428, K), *G. crassifolia* (Ekman 4023, S), *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP), *Actinoseris radiata* (Hatschbach 690, LP), *Chuoa ilicifolia* (López Miranda 1090, LP). —C. Elliptic (left to right): *Gochnatia discoidea* (Blanchet 3345, LP), *G. magna* (Cronquist 11277, NY), *G. spectabilis* (Galrola 32, LP),

Few to several capitula (more than 4) arranged in short-pedunculate to glomerulose pseudocorymbs are found in *Gochnatia arborescens*, *G. magna*, *G. purpusii*, *Gochnatia* sect. *Leucomeris*, *Hyalis lancifolia*, and *Wunderlichia* (*W. bahiensis*, *W. insignis*) (Fig. 2C). Numerous capitula arranged in scapiform, long-pedunculate pseudocorymbs are found in *Gochnatia* sect. *Discoseris* (except *G. suffrutescens*), *Actinoseris* (*A. stenophylla*), *Hyalis argentea*, *Ianthopappus*, and *Wunderlichia senaeii* (Fig. 2D).

*Gochnatia* sect. *Pentaphorus* and *Cyclolepis* have numerous capitula borne in short-pedunculate to glomerulose clusters, that are in turn arranged in leafy pseudoracemes (Fig. 2E). Pseudoracemes in compact or glomerulose clusters, which lack leaves, at the tip of the branches, are characteristic of *Gochnatia palosanto* (Fig. 2F). Loose pseudoracemes are present only in some species of *Pleiotaxis* (e.g., *P. angusterugosa*, *P. gombensis*, *P. oxy-lepis*, *P. racemosa*) (Fig. 2G).

Numerous capitula arranged in glomerulose pseudopanicles are present in most species of *Gochnatia* sect. *Moquiniastrum*, in *G. cordata*, *G. hypoleuca*, and *G. smithii* (Fig. 2H). Short-pedunculate (Fig. 2I) or loose pseudopanicles (Fig. 2J) are present in species of *Gochnatia* sect. *Moquiniastrum* (*G. argentina*, *G. argyrea*, respectively).

#### INVOLUCRE

**Shape.** The involucre shape is either oblong to campanulate or turbinate. Oblong to campanulate involucres are characteristic of most species of *Gochnatia* (Fig. 3A), *Chuoa* (Fig. 3B), *Cnicothamnus* (Fig. 3C), *Cyclolepis* (Fig. 3D), *Hyalis* (Fig. 3E), *Nouelia* (Fig. 3F), *Pleiotaxis* (Fig. 3G), and *Wunderlichia* (Fig. 3H). Turbinate involucres, on the other hand, occur in a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cubensis*, *G. intertexta*, *G. pauciflosculosa*), in some species of *G.* sect. *Hedraiphllum* (*G. hypoleuca*, *G. palosanto*, *G. smithii*) (Fig. 3I), *G. suffrutescens*, *Actinoseris*, and *Ianthopappus* (Fig. 3J).

**Size.** The involucre size ranges from 2 to 45 mm high, with three main categories: (2–)4–7(–8) mm, 10–18 mm, and 20–45 mm high.

(A) The smallest involucres [(2–)4–7(–8) mm] are present in *Gochnatia* sect. *Pentaphorus*, *Gochnatia* sect. *Moquiniastrum* (except *G. argyrea* with 9–10 mm), *G. hypoleuca*, *G. microcephala*, *G. palosanto*, *G. smithii*, *Cyclolepis*, and *Hyalis*.

(B) Intermediate involucres (10–18 mm high) are present in some species of *Gochnatia* (e.g., *G. arborescens*, *G. cordata*, *G. discoidea*, *G. ilicifolia*, *G. magna*, *G. patazina*, *G. purpusii*, *G. recurva*, *G. rotundifolia*, *G. vernonioides*), *Actinoseris*, *Chuoa*, and *Ianthopappus*.

(C) The biggest involucres (20–45 mm) are displayed by a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cowellii*, *G. cubensis*, *G. ekmanii*, *G. picardae*, *G. sagraeana*), *Cnicothamnus*, *Nouelia*, *Pleiotaxis*, and *Wunderlichia*.

**Series of phyllaries.** The phyllaries are arranged in several imbricate series. The highest number is (6)7 to 10 series, and this is found in a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cowellii*, *G. cubensis*, *G. picardae*, *G. recurva*), *G. arborescens*, *Cnicothamnus* (Fig. 3C), *Nouelia* (Fig. 3F), *Pleiotaxis* (Fig. 3G), and *Wunderlichia* (Fig. 3H). Three- to six-seriate involucres occur in most species of *Gochnatia* (Fig. 3A), and *Actinoseris*, *Chuoa* (Fig. 3B), *Cyclolepis* (Fig. 3D), *Hyalis* (Fig. 3E), and *Ianthopappus* (Fig. 3J). *Gochnatia* sect. *Leucomeris* and three species of *G.* sect. *Hedraiphllum* (*G. hypoleuca*, *G. palosanto*, *G. smithii*) show a peculiar feature in their involucres. The capitula are 3- to 4-seriate, but the peduncle bracts extend into the involucre giving a 7- to 12-seriate condition (Fig. 3I).

**Phyllary pubescence and shape.** In almost all the taxa studied the phyllaries are dorsally pubescent or subglabrous. However, *Gochnatia* sect. *Leucomeris*, *G. hypoleuca*, *G. palosanto*, *G. smithii*, and *G. rotundifolia* have dorsally glabrous phyllaries with ciliate margins.

Most genera have linear to oblong or obovate phyllaries with entire margins. *Cnicothamnus* has phyllaries with an apical appendage rounded or rhombic, with lacerate margins (Fig. 3C), and *Wunderlichia* has phyllaries with scarious, colored, and occasionally fimbriate margins (Fig. 3H).

←

*Actinoseris polyphylla* (Hatschbach 35304, LP), *Cnicothamnus lorentzii* (Padaci 84, LP), *Pleiotaxis huillensis* (Gossweiler 10780, US). —D. Linear (left to right): *Gochnatia foliolosa* (Cabrera 3451, LP), *G. argyrea* (Hatschbach 9578, LP), *Hyalis lancifolia* (Schinini 16098, LP), *Actinoseris angustifolia* (Hatschbach 29986, LP), *Pleiotaxis rogersii* (Rolyns 1568, US), *P. dewevrei* (de Hitte 288, US), *Cyclolepis genistoides* (Rojas 7104, LP). Leaf margin. —E. Spinose (left to right): *Chuoa ilicifolia* (López Miranda 1090, LP), *Gochnatia montana* (Ekman 18725, S), *G. enneantha* (Ekman H-15498, S), *G. cubensis* (Ekman 9632, S), *G. intertexta* (Alain A-1680, NY). —F. Denticulate to entire (left to right): *G. polymorpha* (Pereira 8609 & Pabst 7984, LP), *G. rotundifolia* (Handro 157, LP), *G. foliolosa* (Cabrera 3451, LP).

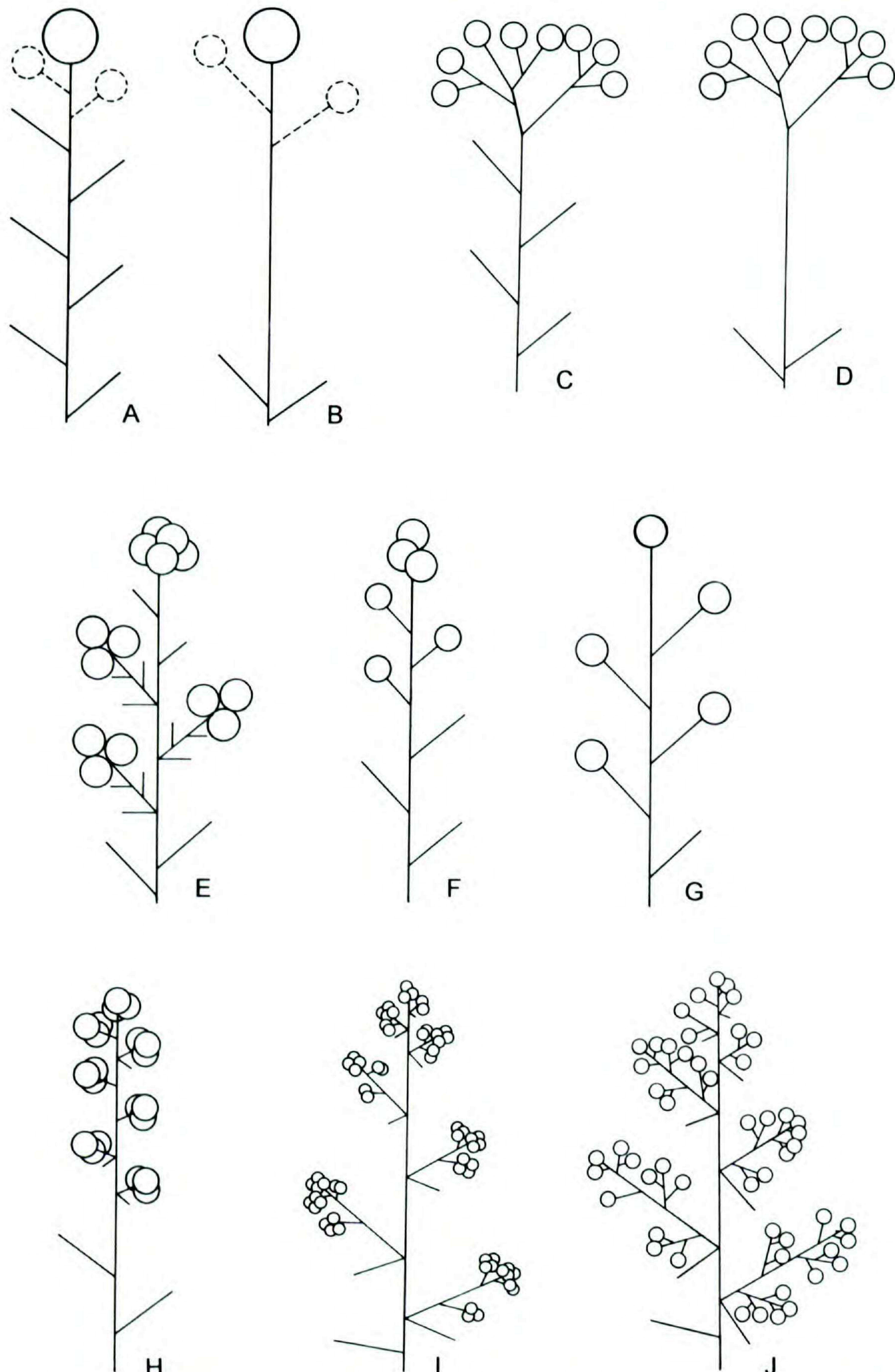


Figure 2. Types of capitulescence. —A. Solitary or few capitula short-pedunculate. —B. Solitary or few capitula long-pedunculate and scapiform. —C. Pseudocorymbs short-pedunculate. —D. Pseudocorymbs long-pedunculate and scapiform. —E. Pseudoracemes glomerulose and leafy. —F. Pseudoracemes apically glomerulose. —G. Loose pseudoracemes. —H. Pseudopanicles glomerulose. —I. Pseudopanicles short-pedunculate. —J. Loose pseudopanicles.

#### PALEAE

*Wunderlichia* is the only genus in the group with receptacular paleae. For this reason, Pruski

(1991) included it in the "Stenopadus group." Cabrera (1971) described *Gochnatia* as typically epaleate, and only exceptionally with some paleae, but mentioned no species. However, we

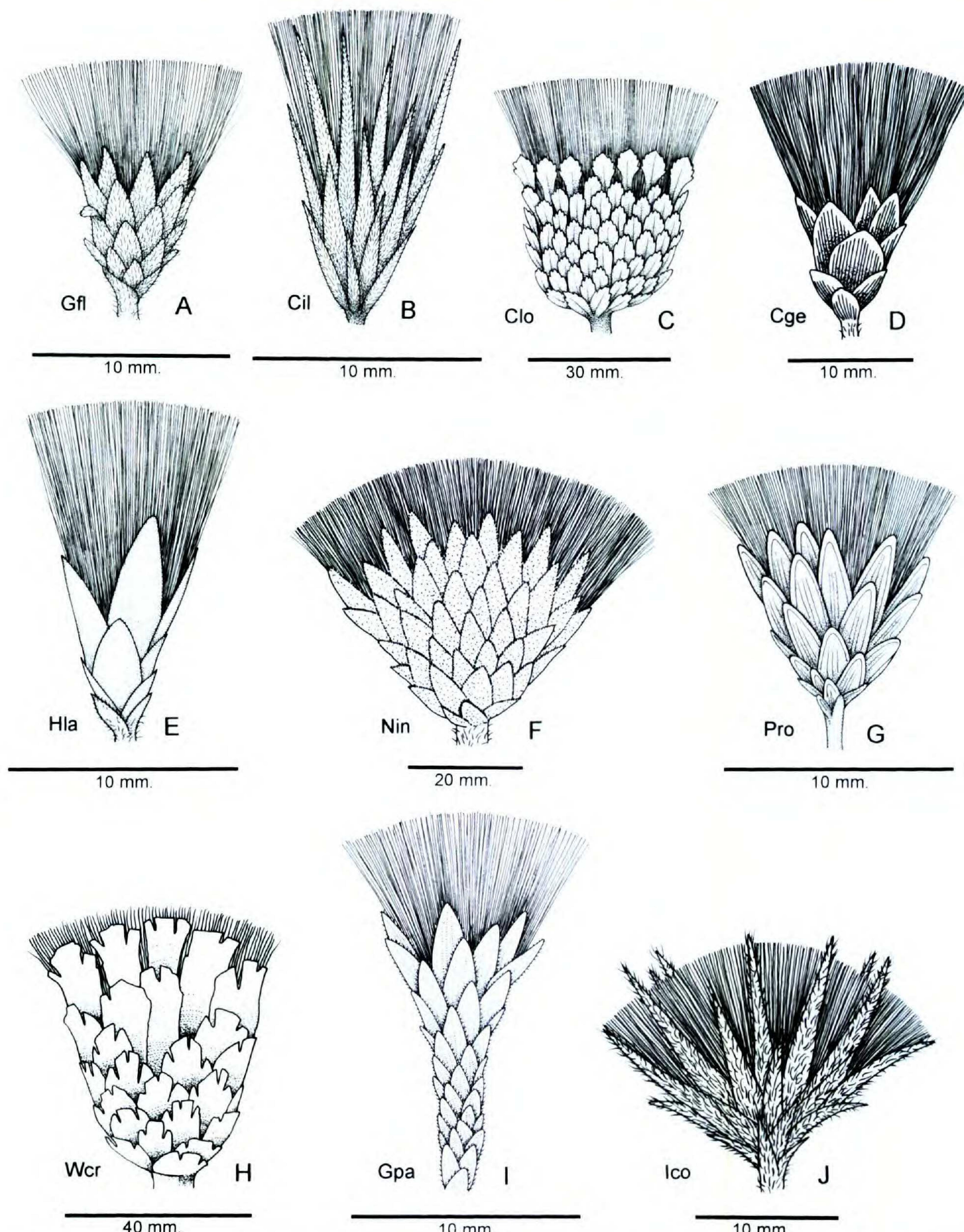


Figure 3. Involucre. A–H. Oblong to campanulate. —A. *Gochnatia floribunda* (Hatschbach 43151, NY). —B. *Chuoa ilicifolia* (López Miranda 1090, LP). —C. *Cnicothamnus lorentzii* (Padaci 84, LP). —D. *Cyclolepis genistoides* (Tinto 2038, LP). —E. *Hyalis lancifolia* (Schinini 16098, LP). —F. *Nouelia insignis* (Maire 2516, NY). —G. *Pleiotaxis rogersii* (Rolyns 1568, US). —H. *Wunderlichia crulsiana* (Ratter et al. 2615, MO). I, J. Turbinate. —I. *Gochnatia palosanto* (Schreiter in 1925, LP). —J. *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP).

found no evidence of paleae in any species of *Gochnatia* examined.

#### FLORETS

*Corolla morphology and sex arrangement.* Corollas in *Gochnatia* and allies may be isomorphic, subdimorphic, or clearly dimorphic.

All florets of the capitula may be hermaphroditic or female (homogamous capitula), or the capitula may have central hermaphroditic florets and marginal female florets (heterogamous capitula). These features are combined as follows:

(A) Corollas isomorphic. Plants with discoid and homogamous capitula made up of hermaphroditic florets with isomorphic tubular corollas are char-

acteristic of most species of *Gochnatia* (Fig. 4A, B), *Chuoa* (Fig. 4C), *Pleiotaxis* (Fig. 4D), and *Wunderlichia* (Fig. 4E). Only *G. argyrea* of section *Moquiniastrum* has isomorphic tubulose corollas and heterogamous capitula (Sancho, 2000). Very occasionally marginal female florets (with staminodes) are found in *Chuoa* (Cabrera, 1955, and our own observations).

(B) Corollas subdimorphic. Such corollas are present only in *Gochnatia* sect. *Moquiniastrum* (except *G. argyrea* and *G. gardneri*) (Fig. 4F) and *Cyclolepis* (Fig. 4G). *Gochnatia* sect. *Moquiniastrum* includes monoecious, polygamous, and gynodioecious plants (Sancho, 2000). Polygamous and gynodioecious species have disciform capitula made up of subdimorphic corollas, i.e., central hermaphroditic florets with tubular actinomorphic corollas and coiled lobes (Fig. 4F<sub>1</sub>), and outer, female florets with tubular subzygomorphic corollas and erect or coiled lobes of different lengths (Fig. 4F<sub>2</sub>). In the gynodioecious genus *Cyclolepis* the female florets have tubular-filiform corollas (Fig. 4G<sub>1</sub>), and the hermaphroditic florets have tubular corollas (Fig. 4G<sub>2</sub>).

(C) Corollas dimorphic. Plants with radiate, homogamous capitula comprising dimorphic, hermaphroditic florets, with outer bilabiate or subbilabiate and central tubular corollas, are present in some species of *Actinoseris* (e.g., *A. polyphylla*, *A. revoluta*, *A. stenophylla*) (Fig. 4H), *Cnicothamnus* (Fig. 4I), *Hyalis* (Fig. 4J), and *Nouelia* (Fig. 4L). Plants with heterogamous capitula and the type of dimorphic corollas previously mentioned are found in *Ianthopappus* (Fig. 4K) and some species of *Actinoseris* (e.g., *A. arenaria*, *A. hatschbachii*, *A. radiata*); the outer florets are female and the central florets hermaphroditic. These truly dimorphic corollas are absent in *Gochnatia*.

It may be noted that tubular, deeply lobed corollas with coiled lobes (reaching up to 2/3 of the corolla) are present in most species of *Gochnatia* (Fig. 4A), and in *Actinoseris*, *Chuoa* (Fig. 4C), *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, and *Pleiotaxis* (Fig. 4D). Tubular, very deeply lobed corollas with straight lobes (more than 2/3 the length of the corolla, almost reaching the base) are present in most Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. calcicola*, *G. cubensis*, *G. gomezii*, *G. oligantha*) (Fig. 4B). Bilabiate corollas have an external 3-dentate lip and an internal 2-cleft lip (3+2 arrangement, e.g., *Actinoseris revoluta*, *Hyalis*, *Ianthopappus*, *Nouelia*) (Fig. 4J–L), and subbilabiate corollas have an external 3-dentate and one entire, internal lip (3+1, e.g., *Acti-*

*noseris hatschbachii*, *A. polyphylla*, *Cnicothamnus*) (Fig. 4H, I).

*Number of florets per capitulum.* The number of florets per capitulum ranges from 4 to 300. A few species of *Gochnatia* (*G. crassifolia*, *G. magna*, *G. recurva*, *G. rotundifolia*, *G. sagræana*) and most species of *Actinoseris*, *Cnicothamnus*, and *Wunderlichia* have 50 to 300 florets per capitulum. Some species of *Gochnatia* (e.g., *G. amplexifolia*, *G. boliviiana*, *G. cordata*, *G. cowellii*, *G. patazina*, *G. vernonioides*), some species of *Actinoseris* (e.g., *A. hatschbachii*, *A. revoluta*), *Ianthopappus*, and *Nouelia* have capitula with 30 to 50 florets. Some species of *Gochnatia* (e.g., *G. arequipensis*, *G. cardenasii*, *G. ilicifolia*, *G. purpusii*), *G.* sect. *Moquiniastrum*, *Chuoa*, and *Cyclolepis* have 7 to 30 florets per capitulum, whereas some species of *Gochnatia* (e.g., *G. hypoleuca*, *G. smithii*), *G.* sects. *Leucomeris* and *Pentaphorus*, a few Caribbean species of *G.* sect. *Gochnatia* (e.g., *G. calcicola*, *G. cubensis*, *G. gomezii*, *G. oligantha*), and *Hyalis* have capitula with 4 to 6 florets.

*Corolla color.* The corollas in *Gochnatia* are predominantly yellow or cream. In some species (e.g., *G. rotundifolia*, *G. decora*, *G. spectabilis*, *G. foliolosa*) they are white and/or lilac. In others (e.g., *G. cowellii*, *G. ilicifolia*, *G. intertexta*, *G. mantuen-sis*, *G. sagræana*) they are orange. The corollas are white, pink, or purple in *Actinoseris*; in *Cnicothamnus* they are orange; in *Chuoa* and *Cyclolepis*, yellow; in *Hyalis* lilac; in *Nouelia* white; in *Pleiotaxis* deep red, pink, white, or cream; in *Wunderlichia* white or yellow. *Ianthopappus* shows white marginal corollas and purple disc corollas.

#### ANTHERS

As well as most species of the tribe Mutisieae, all the taxa in this study have an apical anther appendage and basal tails. The apical appendage can be viewed as an adaptation to protect the pollen in the anther tube from moisture and insect predators until the stigma and style push upward through it for pollen presentation (Stuessy et al., 1996).

With the exception of *Chuoa*, with acute anther appendages (Fig. 5A), anther appendages in *Gochnatia* and related taxa have usually been described as apiculate. *Pleiotaxis* differs in its thickened and bulbous apical appendage (Fig. 5B).

Analysis of this feature in all the genera under study revealed further variation in its shape that is particularly useful in grouping species within *Gochnatia*. The appendage can be short (anthers



Figure 4. A–E. Isomorphic corolla. —A. *Gochnatia magna* (Cronquist 11277, NY). —B. *G. pauciflosculosa* (Eggers 3866, K). —C. *Chuhoa ilicifolia* (López Miranda 1090, LP). —D. *Pleiotaxis dewevrei* (de Hitte 288, US). —E. *Wunderlichia mirabilis* (Martinelli & Stutts 999, NY). F, G. Subdimorphic corolla. —F. *Gochnatia polymorpha* (Hashimoto 624, LP): F<sub>1</sub>, disc corolla, F<sub>2</sub>, marginal corolla. —G. *Cyclolepis genistoides* (Cabrera 3782, LP): G<sub>1</sub>, marginal corolla, G<sub>2</sub>, disc corolla. H–L. Dimorphic corolla. —H. *Actinoseris polyphylla* (Hatschbach 35304, LP): H<sub>1</sub>, disc corolla, H<sub>2</sub>, marginal corolla. —I. *Cnicothamnus lorentzii* (Cabrera et al. 22576, LP): I<sub>1</sub>, marginal corolla, I<sub>2</sub>, disc corolla. —J. *Hyalis lancifolia* (Schinini 16098, LP): J<sub>1</sub>, marginal corolla, J<sub>2</sub>, disc corolla. —K. *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP): K<sub>1</sub>, marginal corolla, K<sub>2</sub>, disc corolla. —L. *Nouelia insignis* (Maire 2516, NY): L<sub>1</sub>, marginal corolla, L<sub>2</sub>, disc corolla.




Figure 5. Apical anther appendage.—A. Not apiculate: *Chuoa ilicifolia* (López Miranda 1090, LP).—B. Apiculate bulbous: *Pleiotaxis eximia* (Rolyns 1836, US). C–F. Caudate anther appendage.—C. *Gochnatia* sect. *Gochnatia* sensu Cabrera (from left to right): *Gochnatia cardenasii* (Cordo & Ferrer 88-B-17, SI), *G. cowellii* (Britton & Cowell 10183, NY), *G. curviflora* (Jeréz et al. 49120, LP), *G. ilicifolia* (Small & Carter 8526, K), *G. montana* (Ekman 18725, S), *G. parvifolia* (Shafer 2938, NY), *G. patazina* (López & Sagástegui 3409, LP), *G. recurva* (León 20946, LP).—D. *Actinoseris*

apiculate) to very long (anthers apically caudate). In addition, it can abruptly terminate in a sharp point, or gradually taper above into an attenuate point. The following three combinations were observed:

(1) Apically caudate (Fig. 5C–E): in most species of *Gochnatia* sect. *Gochnatia* (except *G. boliviensis*, *G. buchii*, *G. microcephala*, *G. tortuensis*, and *G. vernoiooides* with abruptly apiculate apices) (Fig. 5C), *Actinoseris* (Fig. 5D), and *Cnicothamnus* (Fig. 5E).

(2) Attenuate apiculate (Fig. 5G): in *Gochnatia* sect. *Leucomeris*, *G. hypoleuca*, *G. palosanto*, *G. magna*, and *G. rotundifolia*.

(3) Abruptly apiculate (Fig. 5J–L): in *Gochnatia* sect. *Discoseris*, sect. *Moquiniastrum* (short appendage in *G. argentina*, *G. densicephala*, and *G. floribunda*), and sect. *Pentaphorus*, *Gochnatia arborescens*, *G. cordata*, *G. purpusii* (Fig. 5J), *Nouelia* (Fig. 5K), and *Wunderlichia* (very short) (Fig. 5L).

Although useful in distinguishing taxa, some overlap exists between these broad categories such as between apically caudate-attenuate (e.g., *Ianthopappus*, Fig. 5F), attenuate-abruptly apiculate (e.g., *Cyclolepis*, Fig. 5H; *Hyalis*, Fig. 5I), and abruptly apiculate-caudate (e.g., *G. velutina*, Fig. 5J).

Anther tails are free and can be smooth or laciniate. They are smooth in the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. attenuata*, *G. ilicifolia*, and *G. microcephala*), some species of *Gochnatia* sect. *Moquiniastrum* (e.g., *G. barrosii*, *G. densicephala*, *G. floribunda*, *G. paniculata*), some species of *Gochnatia* sect. *Hedraiphillum* (e.g., *G. arborescens*, *G. magna*, *G. purpusii*), *Chuoa*, *Cnicothamnus*, and *Wunderlichia*. The tails are laciniate, at least in one side, in most species of *Gochnatia* (e.g., *G. sect. Discoseris*, *G. sect. Leucomeris*, the South American species of *G. sect. Gochnatia*, and *G. glutinosa*), and in *Actinoseris*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, and *Pleiotaxis*.

## STYLE

Most taxa have smooth styles except for *Wunderlichia* (Fig. 6A) and *Chuoa* (Fig. 6B) with dorsally papillose styles, i.e., with the two branches (rounded and acute at the apex, respectively) covered by short sweeping hairs, and *Pleiotaxis* (Fig. 6C) with a subapical crown of short hairs. All species of *Gochnatia* (Fig. 6D, E), *Actinoseris* (Fig. 6F), *Cnicothamnus* (Fig. 6G), *Cyclolepis* (Fig. 6H), *Hyalis* (Fig. 6I), *Ianthopappus* (Fig. 6J), and *Nouelia* (Fig. 6K) have smooth, apically rounded styles. Most have the inner surface of the branches covered by stigmatic papillae prolonged into the outer surface of the style constituting a ridge of cells, which is less evident in *Cnicothamnus*.

## TRICHOMES

*Leaf pubescence.* Excluding some species such as *Gochnatia rotundifolia*, *Actinoseris hatschbachii*, *A. stenophylla*, and *Hyalis lancifolia*, which have glabrous leaves, at least when mature, there are five different types of trichomes in *Gochnatia* and its relatives.

(1) Oblique septate flagellate hairs: one or two foot cells, one- or more-celled stalks or stipes, and unicellular, very long, flagellate, tubular heads (Fig. 7A). This trichome type is present in most species of *Gochnatia*, *Chuoa*, *Cnicothamnus*, *Pleiotaxis*, and *Wunderlichia*.

(2) Two-armed hairs (or T-shaped, malpighiaceous, anvil, dolabriform hairs): one or two foot cells, uniseriate, generally two- to more-celled stalks, and unicellular heads. The apical cell, which constitutes the head, initially assumes the shape of a hammer and later becomes T-shaped by further outgrowth of the two ends (Fig. 7B, C). This trichome type is present in *Gochnatia* sect. *Moquiniastrum* (Fig. 7B) and *G. cordata*, *Cyclolepis* (Fig.

←

*radiata* (Hatschbach 690, LP). —E. *Cnicothamnus lorentzii* (Ruiz Leal 14162, LP). —F. *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP). —G–I. Attenuate-apiculate anther appendage. G<sub>1</sub>, *Gochnatia* sect. *Leucomeris* sensu Cabrera (from left to right): *Gochnatia decora* (Maung Mya 5309, LP), *G. spectabilis* (Galrola 32, LP). G<sub>2</sub>, *G. hypoleuca* (González Quintero 3215, LP), *G. palosanto* (Schreiter in 1925, LP), *G. magna* (Fernández 3666, NY), *G. rotundifolia* (Joly 596, LP). —H. *Cyclolepis genistoides* (Correa 3172 & Nicora, LP). —I. *Hyalis lancifolia* (Cabrera 4083, LP). —J–L. Abruptly apiculate anther appendage. J<sub>1</sub>, *Gochnatia* sect. *Discoseris* sensu Cabrera (from left to right): *Gochnatia amplexifolia* (Hatschbach 35312, LP), *G. discoidea* (Blanchet 3345, LP). J<sub>2</sub>, *Gochnatia* sect. *Moquiniastrum* sensu Cabrera (from left to right): *G. argyrea* (Hatschbach 9578, LP), *G. densicephala* (Sheperd 5771 et al., UEC), *G. huaniana* (Rojas, herb. Hassler 9752, LP), *G. oligocephala* (Blanchet 3288, US), *G. orbiculata* (Brade 5523, US), *G. paniculata* (Gardner 4810, US), *G. polymorpha* (Glaziou in 1876, LP), *G. velutina* (Smith & Klein 14885, LP), *G. vernoiooides* (López et al. 4364, LP). J<sub>3</sub>, *Gochnatia* sect. *Pentaphorus* sensu Cabrera (from left to right): *G. foliolosa* (Cabrera 3451, LP), *G. glutinosa* (King 183, LP). J<sub>4</sub> (from left to right): *G. arborescens* (Johnston 4023, LP), *G. cordata* (Rambo 545, LP), *G. purpusii* (Purpus 4248, NY). —K. *Nouelia insignis* (Maire 2516, NY). —L. *Wunderlichia azulensis* (Harley et al. 25209, MO) (very shortly apiculate).

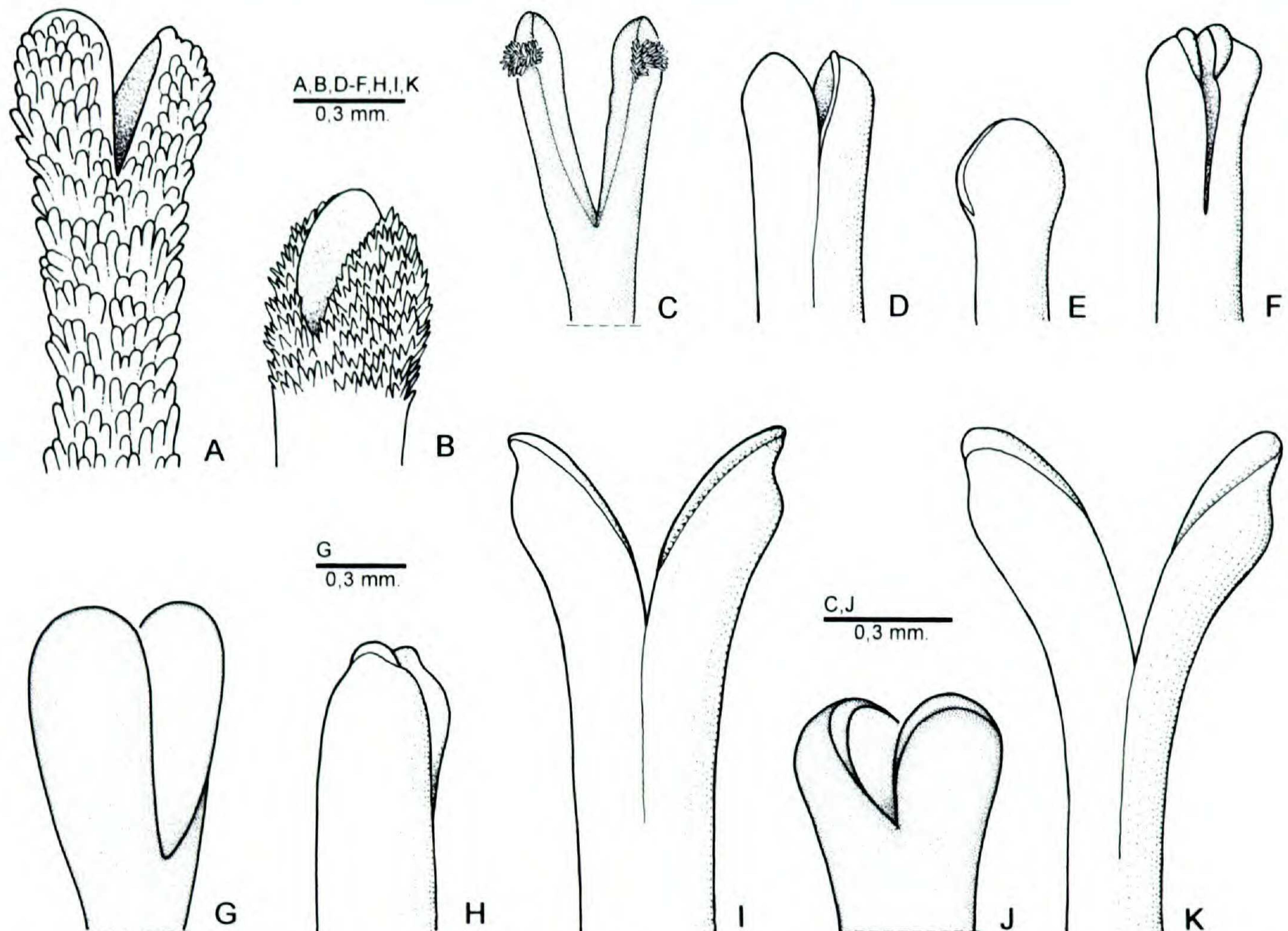


Figure 6. Style branches. —A—C. Papillose style branches. —A. *Wunderlichia azulensis* (Harley et al. 25209, MO). —B. *Chuoa ilicifolia* (López Miranda 1090, LP). —C. *Pleiotaxis eximia* (Rolyns 1836, US). D—K. Smooth style branches. —D. *Gochnatia discoidea* (Blanchet 3345, LP). —E. *G. cordata* (Rambo 545, LP). —F. *Actinoseris angustifolia* (Hatschbach 28756, LP). —G. *Cnicothamnus lorentzii* (Ruiz Leal 14162, LP). —H. *Cyclolepis genistoides* (Zardini & Kiesling 114, LP). —I. *Hyalis argentea* (Ruiz Leal 3701, LP). —J. *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP). —K. *Nouelia insignis* (Maire 2516, NY).

7C), and *Hyalis argentea*. In *Nouelia* one end of the apical cell is very short.

(3) Three- to 5-armed hairs (or 3- to 5-branched, stellate hairs sensu Cabrera, 1971): similar to the 2-armed hairs, but the apical cell has 3 to 5 branches (Fig. 7D). The apical cell does not divide and thus the head remains one-celled. This type is found only in *Gochnatia barrosii* and *G. rusbyana* of section *Moquiniastrum*.

(4) Multistoried T-shaped hairs: similar to the 2-armed hairs, but further periclinal divisions take place in the apical cell. The head is thus comprised of 3 or 4 one-celled layers, all oriented transversally and parallel, but of different lengths (Fig. 7E). This type of trichome, not very common in Asteraceae, has been reported in the tribe Senecioneae (Robinson, 1989). *Ianthopappus* is the only genus with this type of trichome.

(5) Biseriate glandular hairs: comprised of 2 rows of cells in the body, with two to many cells in each row, enclosed by a persistent or collapsed cuticular vesicle (Fig. 7F, G). Glandular hairs are

widespread in all the taxa studied, and especially in species of *Gochnatia* sect. *Pentaphorus* (i.e., *Gochnatia foliolosa*, *G. glutinosa*) where they cover almost the entire surface of the leaf, with the flagellate hairs restricted to the margins.

**Achenial pubescence.** Glabrous or slightly papillose achenes occur in *Chuoa*, in a few species of *Pleiotaxis* (e.g., *P. decipiens*, *P. huillensis*, *P. linearifolia*, *P. welwitschii*), and *Wunderlichia* (e.g., *W. bahiensis*, *W. crulsiana*, *W. insignis*, *W. senaei*). The remaining taxa have villose achenes. Three types of achenial trichomes were found: Duplex or twin hairs, leaf-like hairs (2-armed, oblique-septate flagellate), and glandular hairs.

(1) Duplex or twin hairs: Twin hairs are the common type in Asteraceae, comprised of two triangular or rectangular basal cells, one sometimes reduced, and two cylindrical or elliptical hair cells, equal or subequal in length, generally in contact up to their tips (Hess, 1938; Freire & Katinas, 1995) (Fig. 7H, I). All the taxa studied, in-

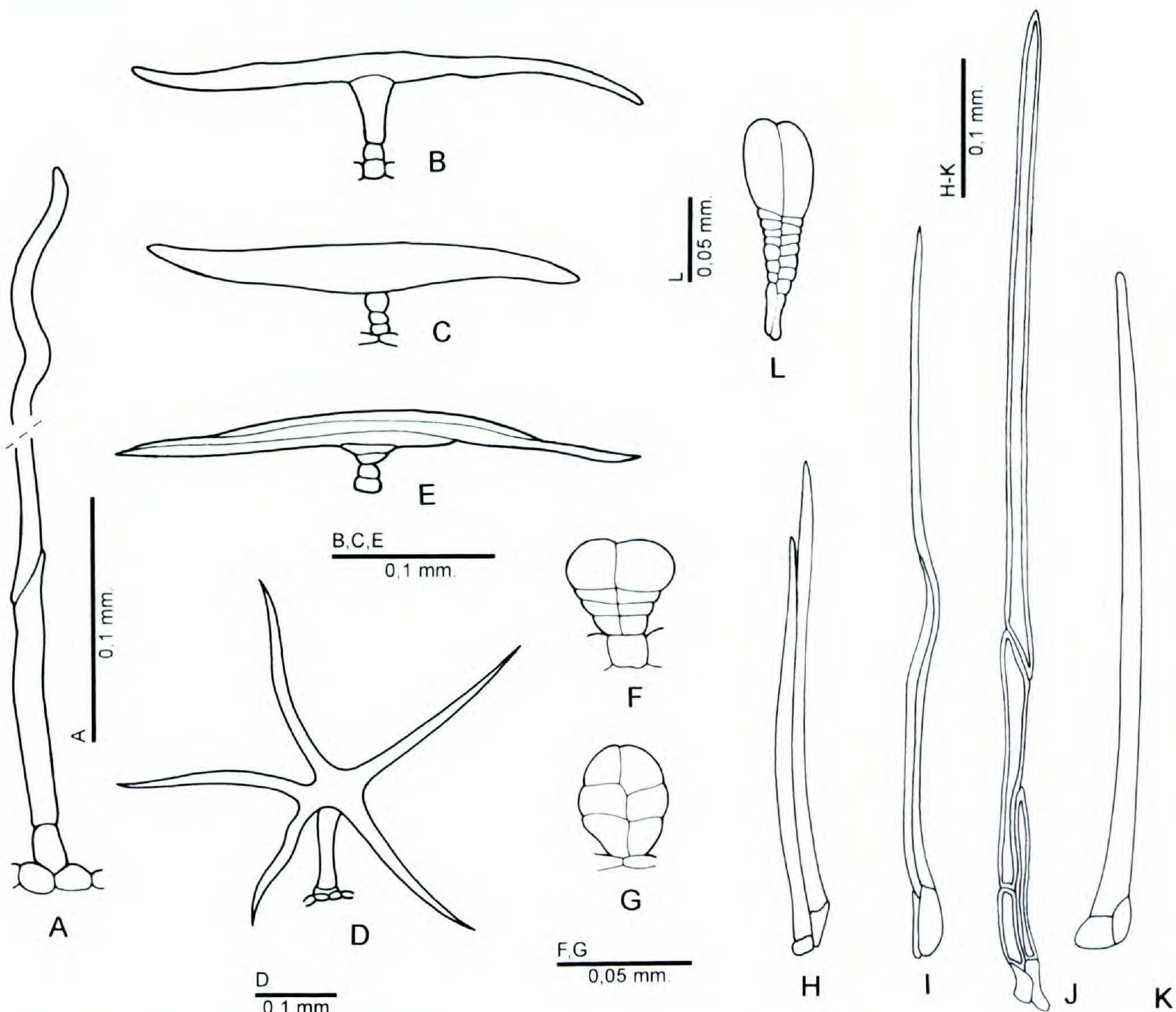


Figure 7. Trichomes. A–G. Leaf hairs. —A. Oblique septate flagellate hair: *Gochnatia tortuensis* (Ekman H-3553, S). —B. *Gochnatia polymorpha* (Pedersen 8587, LP). —C. *Cyclolepis genistoides* (Correa 3172 & Nicora, LP). —D. 3- to 5-armed hair: *Gochnatia barrosii* (Hatschbach 16945, LP). —E. Multistoried T-shaped hair: *Ianthopappus corymbosus* (Palacios & Cuezzo 2304, LP). —F, G. Biseriate glandular hairs. —F. *Gochnatia discoidea* (Blanchet 3345, LP). —G. *Gochnatia glutinosa* (Fabris 1343, LP). H–L. Achenial hairs. H–K. Duplex hairs: *Wunderlichia azulensis* (Harley et al. 25209, MO). H–I. Duplex hairs with one of the hair cells shorter. —J. Septate duplex hair. —K. Duplex hair with only one hair cell. —L. Capitate glandular biseriate hair: *Gochnatia cowellii* (Britton & Cowell 10183, NY).

cluding most species of *Gochnatia*, have achenes with twin hairs, usually very long and filiform. In some cases twin hairs have one hair cell very short (e.g., *Gochnatia purpusii*, *G. recurva*, *G. tortuensis*, *Cyclolepis*, *Wunderlichia azulensis*, *W. mirabilis*) (Fig. 7I), they are septate (e.g., *Gochnatia hatschbachii*, *G. oligocephala*, *Hyalis*, *Pleiotaxis eximia*, *Wunderlichia azulensis*, *W. mirabilis*) (Fig. 7J), or have only one hair cell (*Wunderlichia azulensis*) (Fig. 7K).

(2) Leaf-like hairs: Two-armed hairs in the achenes similar in morphology to the leaf hairs, as described above, were found in *Gochnatia orbiculata*. Only a few species of *Gochnatia* (e.g., *G. cubensis*, *G. magna*, *G. ramboi*) have oblique-septate flagellate hairs.

(3) Achenial biseriate glandular hairs: These are

similar to those on the leaves (Fig. 7F, G) and are very widespread in the group under study, occurring with the other types. A modification of the typical biseriate glandular hair with a very enlarged head, i.e., capitate glandular hair (Metcalfe & Chalk, 1950) (Fig. 7L), was found in the Caribbean species of *Gochnatia* sect. *Gochnatia*.

#### PAPPUS

In all taxa analyzed the pappus is comprised of rigid and scabrid bristles. However, there is interesting variation in bristle length and width, modifications of the lateral cells at the apex of the bristles, and in the number of series of the bristles. Five pappus types were found.

Type A. All the bristles have the same length

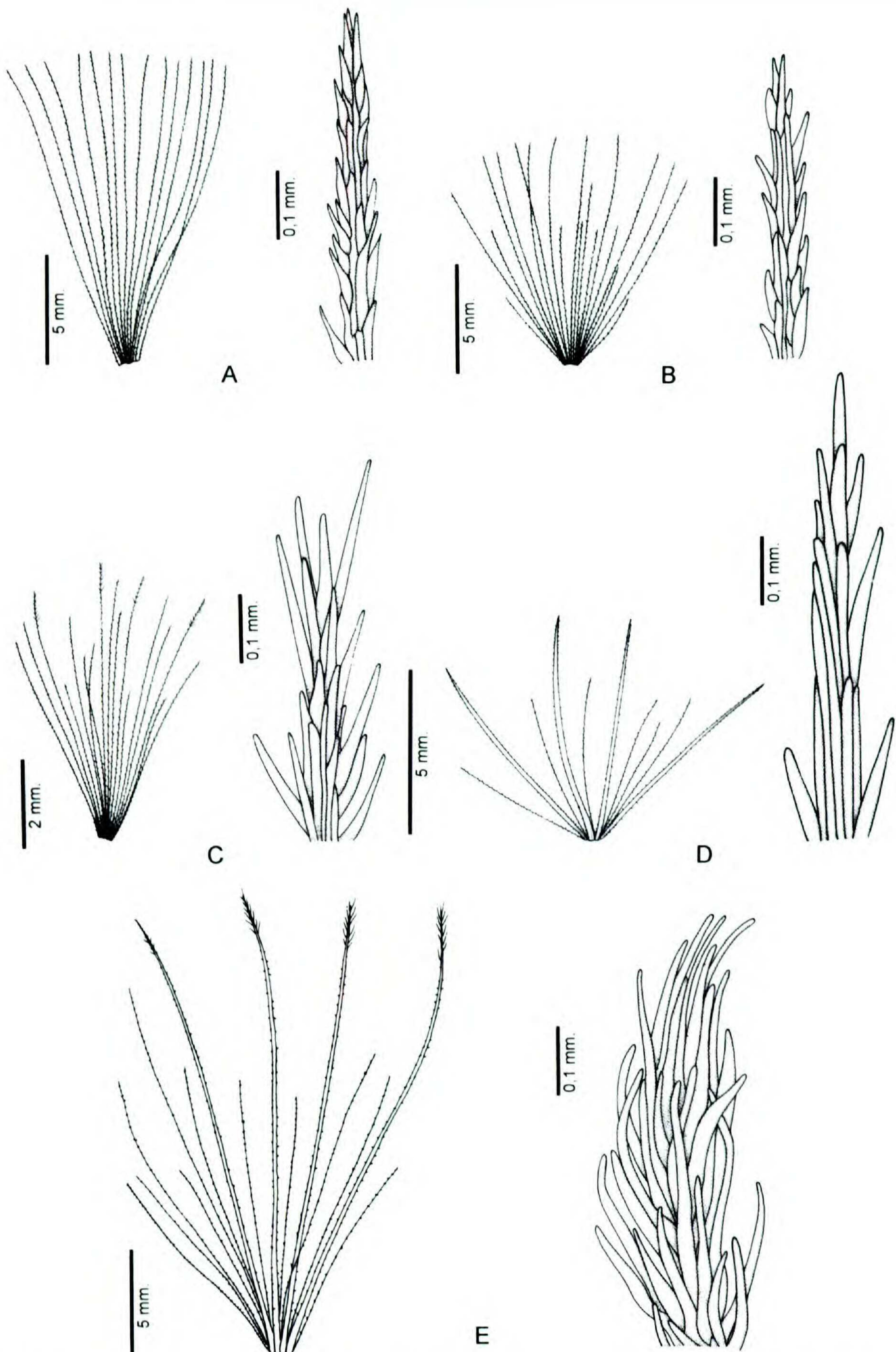


Figure 8. Pappus. General aspect (on the left) and detail of bristle apex (on the right). —A. Type A: *Gochnatia recurva* (León 20946, LP). —B. Type B: *Gochnatia decora* (Maung Mya 5309, LP). —C. Type C: *Gochnatia cordata* (Serrano 6, LP). —D. Type D: *Gochnatia glutinosa* (Fabris 1343, LP). —E. Type E: *Wunderlichia mirabilis* (Irwin et al. 9913, NY).

and width (Fig. 8A). This is present in the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. cubensis*, *G. oligantha*, *G. sagittifera*, *G. tortuensis*), *G.* sect. *Discoseris*, and *Actinoseris*.

*Type B.* All the bristles have the same width, but about half are shorter than the others (Fig. 8B). This type is present in *Gochnatia* sect. *Leucomeris*, the South American species of section *Gochnatia*,

most species of section *Hedraiophyllum*, and *Chuoa*, *Hyalis*, and *Nouelia*.

**Type C.** All the bristles have the same width, half of them are shorter, and the longest are plumose at the apex (Fig. 8C). This pappus is present in *Gochnatia cordata*, *G. sect. Moquiniastrum*, and *Ianthopappus*.

**Type D.** Half of the bristles are long and relatively wide and flat (somewhat paleaceous) and the other half are short and thin (Fig. 8D). This type is present in *Gochnatia* sect. *Pentaphorus* and some species of *Pleiotaxis* (e.g., *P. dewevrei*, *P. eximia*, *P. pulcherrima*), all with the long bristles acute at the apex, and in *Cnicothamnus*, which has the long bristles clavate at the apex.

**Type E.** Half of the bristles are long and relatively wide and flat (somewhat paleaceous) and half are short and thin; all are scabrid, but the longer are plumose at the apex (Fig. 8E). This kind of pappus is found in *Cyclolepis*, some species of *Pleiotaxis* (e.g., *P. huillersii*, *P. rogersii*), and *Wunderlichia*.

The type A pappus, i.e., with all the bristles of the same length, is 1-seriate with 30 to 40 bristles. Types B–E, i.e., with the bristles of different length, are 2- to 3-seriate with more than 50 bristles.

## DISCUSSION

### CHARACTER VALUE

Some characters such as habit, most leaf features, and pappus vary within *Gochnatia*. Other characters, although constant and common to all species of *Gochnatia*, are not exclusive to it, such as multiseriate involucres, tailed anthers with apiculate anther appendages, and smooth style branches. Table 2 shows this and the main morphological characters that allow the genera associated with *Gochnatia* to be distinguished. Some of the characters studied merit a brief discussion.

The involucre of *Gochnatia*, resembling a spruce cone, suggested by Hansen (1991) as a distinguishing character for the group of *Gochnatia* and its associated genera, also occurs in other Mutisieae such as *Aphyllocladus*, *Dinoseris*, *Hyaloseris*, and *Stenopadus*, which are not very closely related to *Gochnatia*. We do not therefore consider that this feature has diagnostic value.

Corolla morphology has been used as a key diagnostic character in Mutisieae. The tubular actinomorphic (Fig. 4A–E), tubular-filiform (Fig. 4G<sub>1</sub>), tubular subzygomorphic (Fig. 4F<sub>2</sub>), subbilabiate (Fig. 4H<sub>2</sub>, I<sub>1</sub>), and bilabiate corollas (Fig. 4J<sub>1</sub>, K<sub>1</sub>,

L<sub>1</sub>) present in the taxa studied show the great variation of this character in Mutisieae. Cabrera (1961, 1977) characterized Gochnatiinae and Barnadesiinae (the latter subtribe currently constitutes the subfamily Barnadesioideae; Bremer & Jansen, 1992) in the first comprehensive key to subtribes of Mutisieae by having more or less actinomorphic, deeply 5-lobed disc corollas, with equal or unequal segments, but never truly bilabiate, and bilabiate or subligulate ray corollas. The Mutisiinae and Nassauviinae, on the other hand, have clearly bilabiate (the disc florets exceptionally actinomorphic) or ligulate disc and ray florets. According to this key all the taxa studied, although variable in their corollas, would correspond to the subtribe Gochnatiinae (sensu Cabrera, 1977). Other authors (e.g., Robinson, 1991; Bremer, 1994) regard the distinction between Gochnatiinae and Mutisiinae, based only on the actinomorphic versus bilabiate disc florets, to be artificial and recognize only Mutisiinae sensu lato.

Apiculate anther appendages have been strongly considered to be an advanced character within Mutisieae (Cabrera, 1977; Hansen, 1991; Karis et al., 1992; Bremer, 1994). The shape of the anther appendage, i.e., caudate, attenuate, and abruptly apiculate (Fig. 5C–L), led to distinction within *Gochnatia* and also among genera. Indeed, *Gochnatia* can be associated with *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, and *Wunderlichia* by the common possession of flat (not bulbous), apiculate anther appendages. *Chuoa* and *Pleiotaxis* (Fig. 5A, B), based on their acute and bulbous anther appendages, respectively, are very different. The current tribal position of *Pleiotaxis* is controversial. Some authors regard *Pleiotaxis* as forming part of a mutisiean “Dicoma-group” (Bremer, 1994; Ortiz, 2000; Ortiz & Coutinho, 2001). According to Hansen (1991), this group of genera (including *Pleiotaxis*) should be excluded from Mutisieae by features of style branches, anthers, and pollen type.

Smooth styles are revealed as another informative feature in this group of taxa, although the value of this character is controversial. Some authors (Bremer, 1987) consider the glabrous styles to be plesiomorphic within Asteraceae (although the Lobeliaceae, characterized by hairy style branches, were used as an outgroup), while others (Stuessy et al., 1996) postulate the smooth condition to be derived with Calyceraceae as the outgroup. At present the hypothesis that Calyceraceae are the sister group of Asteraceae (e.g., Albach et al., 2001; Urribarri & Stuessy, 2001) is widely accepted. Since the style branches in Calyceraceae are papillose

Table 2. Main morphological characters that allow the distinction of *Gochnertia* and associated genera. The exclusive characters are in boldface. Uncommon features are in parentheses. Characters that distinguish *Gochnertia* from other genera are in *italics*.

	<i>Gochnertia</i>	<i>Actinoseris</i>	<i>Chuoa</i>	<i>Cnicothamnus</i>	<i>Cyclolepis</i>	<i>Hyalis</i>	<i>Ianthopappus</i>	<i>Nouelia</i>	<i>Pleiotaxis</i>	<i>Wunderlichia</i>
Habit	trees, shrubs, (subshrubs)	herbs	shrubs	trees	<b>spinose,</b> <b>aphyllous</b>	subshrubs	subshrubs	shrubs	herbs	trees
Non-glandular foliar tri- chomes	flagellate, 2- armed, <b>3-</b> <b>to 5-</b> <b>armed</b>	flagellate	flagellate	flagellate	2-armed	<b>2-armed</b>	<b>multistoried</b>	<b>2-armed</b>	<b>T-shaped</b>	flagellate
Receptacle Capitula	epaleate <i>homogamous</i>	epaleate <i>homogamous,</i> ( <i>heteroga-</i> <i>mous</i> )	epaleate <i>homogamous,</i> ( <i>heteroga-</i> <i>mous</i> )	epaleate <i>homogamous</i>	epaleate <i>homogamous</i>	epaleate <i>homogamous</i>	epaleate <i>homogamous</i>	epaleate <i>homogamous</i>	epaleate <i>homogamous</i>	<b>paleate</b> <i>homogamous</i>
Phyllaries apical appendage Corolla	absent	absent	absent	<b>rhombic,</b> <b>lacerate</b>	absent	dimorphic	subdimorphic	dimorphic	dimorphic	isomorphic
Corolla color	<i>isomorphic</i>	dimorphic	isomorphic	dimorphic	orange	yellow	lilac	white and purple	white	white, yellow
Anther apical appendage	<i>apiculate:</i> yellow, cream (lilac, or- ange, white)	white, pink, purple	yellow	<b>acute</b>	<i>apiculate:</i> abruptly, caudate	<b>smooth</b>	laciniate	laciniate	smooth	red, pink, white, cream
Anther tails	<i>smooth</i>	smooth	smooth	<i>smooth</i>	<i>apiculate:</i> abruptly- attenuate	<b>smooth</b>	laciniate	laciniate	smooth	<b>apiculate:</b> <b>thick-</b> <b>ened, bul-</b> <b>bose</b>
Style branches	<i>smooth</i>	<i>smooth</i>	<i>smooth</i>	<b>pubescent:</b> <b>dorsally</b>	<i>caudate</i>	<i>smooth</i>	smooth	smooth	<b>pubescent:</b> <b>subapical-</b> <b>ly</b>	Type E
Pappus	Types A, B, C, D	Type A	Type B	Type D	Type E	Type B	Type C	Type D	Type E	Type E

(Hansen, 1992, and our own observations) the smooth style branches in Asteraceae become an advanced character for the family.

The multistoried T-shaped hair (Fig. 7E), the 2-, and 3- to 5-armed hairs (Fig. 7B–D), the capitate glandular achenial hair (Fig. 7L), and the pappus types established here (Fig. 8) are revealed as new diagnostic characters. In fact: (1) the multistoried T-shaped hair is exclusive to *Ianthopappus* and becomes another character to distinguish it; (2) the 2-armed hairs are present in *Gochnatia cordata*, *G.* sect. *Moquiniastrum*, *Cyclolepis*, *Hyalis*, and *Nouelia*; (3) the 3- to 5-armed hairs are exclusive to some species of *Gochnatia* sect. *Moquiniastrum*; (4) the capitate glandular achenial hairs, with a very enlarged head, distinguish most of the Caribbean species of *Gochnatia* sect. *Gochnatia*; and (5) pappus types A, B, C, D are present in *Gochnatia* and allow the distinction of sections within the genus (see below), while type E is present only in *Cyclolepis*, *Pleiotaxis*, and *Wunderlichia*.

#### CIRCUMSCRIPTION OF *GOCHNATIA* AND ITS SECTIONS

Our morphological analysis confirms that *Gochnatia* has no single exclusive feature that distinguishes it from related taxa, but it can be defined by a set of characters, i.e., homogamous (rarely heterogamous) capitula, isomorphic (tubular) to subdimorphic (tubular and tubular subzygomorphic) corollas, apiculate anther appendages, and smooth style branches (Table 2).

After analyzing the morphological features of *Gochnatia*, the sections established by Cabrera (1971) were reviewed and some changes are proposed.

The distinctiveness of two of the six Cabrera sections, sect. *Discoseris* and sect. *Pentaphorus*, was confirmed and additional characters supporting them were found. For instance, *Discoseris* has pappus type A and *Pentaphorus* type D.

*Gochnatia cordata*, placed by Cabrera in section *Hedraiphyllum*, has characters that link it to section *Moquiniastrum* such as the 2-armed foliar hairs (Fig. 7B), numerous capitula arranged in glomerulose pseudopanicles (Fig. 2H), and pappus type C (Fig. 8C) and must be included in this section. However, it constitutes the type species of section *Hedraiphyllum* established by Lessing (as a subgenus) in 1832 and has priority over the name of section *Moquiniastrum* established by Cabrera in 1971 (with *G. polymorpha* as the type species). Thus, the name *Hedraiphyllum* is retained in what was known until now as section *Moquiniastrum*.

The remaining three sections sensu Cabrera,

sect. *Gochnatia*, sect. *Hedraiphyllum*, and sect. *Leucomeris*, are redefined resulting in the establishment of five sections: sect. *Anastraphioides*, sect. *Glomerata*, sect. *Gochnatia*, sect. *Leucomeris*, and sect. *Rotundifolia*.

Cabrera (1971) established two groups in his key to section *Gochnatia*, the “South American species” and the “Caribbean species.” Species of this section have some characters in common, such as solitary or 2 to 3 capitula and caudate anther appendages, but other characters suggest that it should be separated into two sections: sect. *Anastraphioides* and sect. *Gochnatia*. The Caribbean species form the new section *Anastraphioides* clearly differentiated by spiny leaf margins (Fig. 1E), corollas very deeply 5-lobed (Fig. 4B), and pappus type A (Fig. 8A). The South American species, on the other hand, have predominantly ovate leaves with entire margins (Fig. 1A, F), corollas deeply 5-lobed, and pappus type B (Fig. 8B), and correspond to section *Gochnatia*.

The species *Gochnatia rotundifolia*, included by Cabrera in section *Gochnatia*, has characters that show a departure from the other sections of the genus such as glabrous and 3-veined leaves, white corollas, and anther appendages attenuate. It would approach Cabrera’s section *Leucomeris* by its phyllaries glabrous with ciliate margins and conspicuous parallel veins, but *G. rotundifolia* lacks the involucre extending into the peduncle typical of this section. Consequently, this species is placed in the new, monotypic section *Rotundifolia*.

*Gochnatia* sect. *Hedraiphyllum* sensu Cabrera, which was already recognized by Cabrera (1971) to be artificial, is split off. Three species of this section, *G. arborescens*, *G. magna*, and *G. purpusii*, are placed in the new section *Glomerata* characterized by the exclusive presence of numerous capitula arranged in glomerulose pseudocorymbs (Fig. 2C). As mentioned above, the type species of section *Hedraiphyllum*, *G. cordata*, was moved to Cabrera’s *Gochnatia* sect. *Moquiniastrum*. The remaining species of section *Hedraiphyllum*, *G. hypoleuca*, *G. palosanto*, and *G. smithii*, were placed in section *Leucomeris* largely based on their involucre with glabrous, conspicuously veined phyllaries, ciliolate at the margins, extending into the peduncle (Fig. 3I).

In summary, we propose the following eight sections for the genus *Gochnatia*: sect. *Anastraphioides*, sect. *Discoseris*, sect. *Glomerata*, sect. *Gochnatia*, sect. *Hedraiphyllum*, sect. *Leucomeris*, sect. *Pentaphorus*, and sect. *Rotundifolia*. This new infrageneric classification, with descriptions and a key to the sections, is shown in Appendix 2.




Figure 9. Main morphological characters defining the *Gochnati* complex, allowing the distinction of *Gochnati* from its related taxa, and also sections within *Gochnati*.

THE *GOCHNATIA* COMPLEX

The combination of apiculate anther appendages and smooth style branches is exclusive to *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, and *Nouelia* within Mutisieae. Consequently, these genera are recognized here as the *Gochnatia* complex (Fig. 9). *Chuoa*, *Pleiotaxis*, and *Wunderlichia*, as already mentioned, differ in their styles and anthers.

Within the *Gochnatia* complex, the genus most morphologically similar to *Gochnatia* is *Cyclolepis*. This genus shares trichomes 2-armed, subdimorphic corollas, and gynodioecy with section *Hedraiophyllum*, which constitutes a pivotal group among the remaining species of *Gochnatia* and *Cyclolepis*, providing a "link" between both genera. *Cyclolepis*, however, can be distinguished from *Gochnatia* by its leafless, spiny branches, tubular, filiform female florets (Fig. 4G<sub>1</sub>), and pappus type E (Fig. 8E).

The hypothesis that a shrubby habit, large, homogamous, and solitary or few capitula, with yellow, and actinomorphic corollas represent primitive conditions in Asteraceae has been widely discussed and recognized (Maguire & Wurdack, 1957; Carlquist, 1976; Bremer, 1987, 1994; Pruski, 1991; Stuessy et al., 1996). From this point of view, most species of *Gochnatia* have a set of plesiomorphic characters when compared with the remaining genera of the complex. This hypothesis is consistent with Cabrera's (1977) idea that *Gochnatia* is the basal genus in a complex from which the other genera in the subtribe are derived.

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#### APPENDIX I.

Index to specimens examined, with vouchers. Note: During preparation of this work, the new species *Gochnatia lanceolata* Beltrán & Ferreyra was published (Beltrán & Ferreyra, 2001). Specimens examined of this species (*Carolina* 01, isotype, US; *Torrice* & *Peca* 336, US) have pubescent styles and acute anther appendages, so this species must be excluded from *Gochnatia* and does not belong to the *Gochnatia* complex.

#### *Actinoseris*

- A. angustifolia*: BRAZIL. **Minas Gerais**: Jaboticatuba, Hatschbach 28756 (LP); Serra do Cipó, Hatschbach 29986 (LP).
- A. polymorpha*: BRAZIL. **Minas Gerais**: Serra de Cipó, Brade 2007 (LP).
- A. polyphylla*: BRAZIL. **Minas Gerais**: Santa Ana do Riacho, Hatschbach 35304 (LP).
- A. radiata*: BRAZIL. **Paraná**: Campo Largo, Hatschbach 690 (LP).
- A. stenophylla*: BRAZIL. **Minas Gerais**: Santa Ana do Riacho, Hatschbach 35388 & Kocicki (LP).

#### *Cyclolepis*

- C. genistoides*: PARAGUAY. Chaco Paraguayo, Rojas 7104 (LP). ARGENTINA. **Salta**: Quebrada de las Conchas, Cabrera 3782 (LP). **Río Negro**: Gral. Conesa, Correa 3172 & Nicora (LP). **Salta**: La Candelaria, Schreiter 6630 (LP). **San Juan**: La Laja, Tinto 2038 (LP). **Neuquén**: Plotier, Banda, Zardini & Kiesling 114 (LP).

#### *Chuoa*

- C. ilicifolia*: PERU. **La Libertad**: Santiago de Chuco, López Miranda 1090 (LP).

#### *Cnicothamnus*

- C. azafran*: ARGENTINA. **Salta**: Serranías del Crestón, Bortagaray 226 (LP). **Jujuy**: Santa Bárbara, Cabrera et al. 26287 (LP).
- C. lorentzii*: ARGENTINA. **Salta**: Caldera, Cabrera et al. 22576 (LP); Capital, Cerro San Bernardo, Padaci 84 (LP); Abra de Santa Laura, Ruiz Leal 14162 (LP); Capital, Bonavía 61 (LP); camino de cornisa Salta-Jujuy, Zardini 1292 (LP).

#### *Gochnatia*

- G. amplexifolia*: BRAZIL. **Minas Gerais**: Santa Ana do Riacho, Hatschbach 35312 (LP).
- G. arborescens*: MEXICO. **Baja California**: Isla Cerralvo, Johnston 4023 (LP); entre Santonio y Puerto de Bahía de los Muertos, Wiggins 5632 (US); along the Pacific Coast, 14 mi. S of Pescadero, Spjut & Edson 6085 (US).
- G. arequipensis*: PERU. **Arequipa**: Monte Chiwata, Eyerdam & Beetle 22120 (LP).
- G. argentina*: ARGENTINA. **Tucumán**: Trancas, Meyer 22421 (LP). **Entre Ríos**: Paracao, Paraná, Schulz 173 (LP); Leales, Venturi 703 (LP).
- G. argyrea*: BRAZIL. **Paraná**: Vila Velha, Dusén 4035 (LP), Dusén 9115 (G), Hatschbach 9578 (LP).
- G. attenuata*: CUBA. **Oriente**: Sierra de Nipe, Ekman 19174 (LP).

- G. barrosii*: BRAZIL. **Paraná**: Cianorte, *Hatschbach* 16945 (LP). **Minas Gerais**: Ituitaba, *Macedo* 1138 (LP). PARAGUAY. **Amambay**: Parque Nacional Cerro Corá, *Sancho* 8 (LP).
- G. blanchetiana*: BRAZIL. **Ceará**: Serra do Araripe, *Gardner* 1735 (K). **Goiás**: *Glaziou* 21663 (G).
- G. boliviensis*: BOLIVIA. **Santa Cruz**: Florida, *Cabrera & Gutiérrez* 33804 (LP).
- G. buchii*: DOMINICAN REPUBLIC. Falda del Morro, Monte Cristo, *Jiménez* 1598 (LP).
- G. calcicola*: CUBA. **Oriente**: Guantánamo, *Ekman* 15764 (S).
- G. cardenasii*: ARGENTINA. **Jujuy**: Tafna, *Cordo & Ferrer* 88-B-17 (SI).
- G. cordata*: ARGENTINA. **Entre Ríos**: Federación, *Burkart* 23169 & *Crespo* (LP); Santa Ana, *Serrano* 6 (LP). BRAZIL. **Rio Grande do Sul**: Porto Alegre, *Rambo* 545 (LP).
- G. cowellii*: CUBA. **Santa Clara**: Santa Clara, *Britton & Cowell* 10183 (NY).
- G. crassifolia*: CUBA. **Oriente**: Baracoa, *Ekman* 4023 (S).
- G. cubensis*: CUBA. **Oriente**: Sierra de Nipe, *Ekman* 4767 (S), 9632 (S).
- G. curviflora*: BOLIVIA. **Tarija**: Tarija, *Fiebrig* 2838 (LP). ARGENTINA. **Jujuy**: Humahuaca, *Meyer* 21409 (LP). **Salta**: La Candelaria, *Schreiter* 9409 (LP); La Candelaria, *Jeréz et al.* 49120 (LP).
- G. decora*: MYANMAR. **Bhamo**: Lweji, *Maung Mya* 5309 (LP).
- G. densicephala*: BRAZIL. **Rio de Janeiro**: Río de Janeiro, *Glaziou* 11072 (K). **Minas Gerais**: Poços de Caldas, *Leoncini* 88 (LP); Pico da Bandeira, *Shepherd* 5771 *et al.* (UEC).
- G. discoidea*: BRAZIL. **Bahia**: Igregia Velha, *Blanchet* 3345 (LP).
- G. discolor*: BRAZIL. **Minas Gerais**: *Claussen* 1301 (NY), *Claussen* in 1840 (K).
- G. ekmani*: CUBA. Sin. loc., *Wright* 2875 (GH).
- G. enneantha*: DOMINICAN REPUBLIC. Cordillera Central, Samaná, Los Haitises, *Ekman* H-15498 (S).
- G. floribunda*: BRAZIL. **Minas Gerais**: Morro do Frío, *Gardner* 4806 (K); Diamantina, *Hatschbach* 30192 (US). **Distrito Federal**: Brasilia, *Hatschbach* 43151 (NY).
- G. foliolosa*: CHILE. **Santiago**: Cerro Renca, *Cabrera* 3451 (LP). **Valparaíso**: El Quisco, *Mahu* 10336 (LP).
- G. gardneri*: BRAZIL. **Goyaz**: Capella da Passe, *Gardner* 4183 (K).
- G. glutinosa*: ARGENTINA. **Tucumán**: Tafí, *Fabris* 1343 (LP). **Mendoza**: Cerro de La Gloria, *King* 183 (LP).
- G. gomezii*: CUBA. **Oriente**: Región de Moa, Cerro Miraflores, *Marie-Victorin et al.* 21591 (GH).
- G. hatschbachii*: BRAZIL. **Minas Gerais**: Jaboticatubas, *Hatschbach* 29951 (LP); Datas, *Hatschbach* 30155 (LP).
- G. haumaniana*: BRAZIL. **Mato Grosso do Sul**: Ponta Porá, *Meyer* 18770 (LP). PARAGUAY. **Amambay**: Sierra de Amambay, *Rojas* 6575 (LP), *Rojas* [herb. *Hassler* 9752] (G); Est. Los cinco hermanos, *Sancho* 41 (LP).
- G. hypoleuca*: MEXICO. **Hidalgo**: Cañada del Vaquero, *González Quintero* 3215 (LP). **Coahuila**: Sierra Gavia, *Johnston* 7223 (LP).
- G. ilicifolia*: BAHAMAS ISLANDS. **Andros Island**: Coprice, *Small & Carter* 8526 (K).
- G. intertexta*: CUBA. **Pinar del Río**: Cajalbana, *Alain A-* 1680 (NY).
- G. magna*: MEXICO. **San Luis Potosí**: *Cronquist* 11277 (NY); Queretaro, 5 km SW Jalpan, *Fernández* 3666 (NY).
- G. mantuensis*: CUBA. **Pinar del Río**: Guane, *Shafer* 11208 (LP).
- G. microcephala*: CUBA. **Oriente**: Boca Guantánamo a Mantua, *Bro. Hioram* 4874 (NY).
- G. mollissima*: BRAZIL. **Rio Grande do Sul**: *Malme* 648 (S); pr. Santa María, *Malme* 1261 (S).
- G. montana*: CUBA. **Pinar del Río**: Guane, *Ekman* 18725 (S).
- G. obtusifolia*: CUBA. **Oriente**: Southern Baracoa region, Mesa de Prada, *León* 11963 (NY).
- G. oligantha*: REPUBLICA DOMINICANA. Monte Cristi, N of Villa Isabel, *Jiménez* 3614 (US).
- G. oligocephala*: BRAZIL. **Bahia**: Serra do Jacobina, *Blanchet* 3288 (US); Río Branco, *Curran* 284 (NY), *Salzmann s.n.* (G).
- G. orbiculata*: BRAZIL. **São Paulo**: Moóca, *Brade* 5523 (US). **Rio Grande do Sul**: Guaiba, *Sancho* 48 (LP); río Jaquety hills, *Tweedie* 998 (K).
- G. palosanto*: ARGENTINA. **Jujuy**: San Pedro, *Cabrera & Fabris* 21157 (LP). **Tucumán**: Vipos, Trancas, *Venturi* 1296 (LP), *Schreiter* in 1925 (LP).
- G. paniculata*: BRAZIL. **Minas Gerais**: Massa, *Brade* 13550 (LP), *Gardner* 4810 (US).
- G. parvifolia*: CUBA. **Oriente**: Barren Savannas, *Shafer* 2938 (NY).
- G. patazina*: PERU. **La Libertad**: Pataz entre Huayllillas y Tayabamba, *López & Sagástegui* 3409 (LP).
- G. pauciflosculosa*: BAHAMAS ISLANDS. **Fortune Island**: *Eggers* 3866 (K); Mariguana Island, 10 mi. W of Abraham Bay, *Wilson* 7428 (K).
- G. picardae*: HAITI. Massif de la Selle, croix-des Bauquets, gorge of Grande-Rivière de cul-de-sac, *Ekman H-5385* (K).
- G. polymorpha*: BRAZIL. **Rio de Janeiro**: Tijuca, *Glaziou* in 1876 (LP). **São Paulo**: Paranaiba do Sul, *Hashimoto* 624 (LP). **Rio Grande do Sul**: *Pereira* 8609 & *Pabst* 7984 (LP). PARAGUAY. **Amambay**: *Sancho* 26, *Sancho* 32 (LP). **San Pedro**: Lima, *Pedersen* 8587 (LP).
- G. pulchra*: BRAZIL. **São Paulo**: Campos de Emas, *Cabrera* 12311 (LP); Ityrapina, *Gehrt* 8296 (LP).
- G. purpusii*: MEXICO. **Puebla**: Tehuacán, *Purpus* 4248 (NY).
- G. ramboi*: BRAZIL. **Santa Catarina**: Xanxeré, *Rambo* 50005 (S). **Rio Grande do Sul**: Palmeira, *Rambo* 51961 (LP).
- G. recurva*: CUBA. **Oriente**: entre Moa y Punta Andén, *León* 20946 (LP).
- G. rotundifolia*: BRAZIL. **São Paulo**: Capital, Jabaquara, *Handro* 157 (LP); Vila Esperança, *Joly* 596 (LP).
- G. rusbyana*: BOLIVIA. **Yungas**: Bang 2252 (LP). PERU. **Cusco**: Alto Urumbamba, *Zamalloa* 2015 (LP).
- G. sagræana*: CUBA. **Habana**: *León* 7094 (NY); Vedado, *Alain* 2532 (NY).
- G. shaferi*: CUBA. **Oriente**: La Caridad, *López Figueiras* 1738 (NY).
- G. smithii*: MEXICO. **Oaxaca**: Cuesta de Coyula, *Conzatti* 4135 (US).
- G. sordida*: BRAZIL. **Paraná**: Ponta Grossa, *Hatschbach* 17422 (LP); Senges, *Hatschbach* 27167 (K).
- G. spectabilis*: INDIA. **Uttar Pradesh**: Rajpur, Dehra Dun District, *Galrola* 32 (LP).

*G. tortuensis*: HAITI. Presquile du Nord-Ouest, Port-de Paix, *Ekman* H-3553 (S).

*G. vargasii*: PERU. Apurimac: Abancay, Vargas 16317 (LP).

*G. velutina*: BRAZIL. Paraná: Ponta Grossa, Vila Velha, Hatschbach 23447 (LP), López 4364 (LP), Smith & Klein 14885 (LP).

*G. vernonioides*: PERU. Amazonas: Chachapoyas, Tingo, Ferreyra 7097 (LP); entre Chachapoyas y Leimebamba, López et al. 4364 (LP). La Libertad: Bolívar, Infantes 1701 (LP), López & Sagástegui 3354 (LP).

### Hyalis

*H. argentea*: ARGENTINA. Mendoza: Tupungato, Ruiz Leal 3701 (LP).

*H. lancifolia*: ARGENTINA. Chaco: San Fernando, Cabrera 4083 (LP), Schinini 16098 (LP).

### Ianthopappus

*I. corymbosus*: ARGENTINA. Corrientes: Paso Troncón, Palacios & Cuezzo 2304 (LP).

### Nouelia

*N. insignis*: CHINA. Maire 2516 (NY). Yunnan: l' Abbe Delavay 2498 (US), Rock 11714 (US).

### Pleiotaxis

*P. dewevrei*: DEMOCRATIC REPUBLIC OF CONGO. Lukulu, de Hitte 288 (US).

*P. eximia*: DEMOCRATIC REPUBLIC OF CONGO. Tshinloingwe (Haut Katanga), Rolyns 1836 (US). ZIMBABWE. 20 km de Mangula, Lavranos 22745 (US).

*P. huillensis*: ANGOLA. Huila, Hampata, Gossweiler 10780 (US).

*P. pulcherrima*: ANGOLA. Distr. do Cuanza Sul, Seles, Gossweiler 9367 (US).

*P. rogersii*: ZAIRE—DEMOCRATIC REPUBLIC OF CONGO. Elisabethville, Rolyns 1568 (US).

### Wunderlichia

*W. azulensis*: BRAZIL. Minas Gerais: Pedra Azul, Harley et al. 25209 (MO).

*W. crulsiana*: BRAZIL. Goiás: Chapada dos Veadeiros, Ratter et al. 2615 (MO).

*W. mirabilis*: BRAZIL. Goiás: Serra do Cristais, Irwin et al. 9913 (NY); about 52 km W of Alto Paraiso, Martinelli & Stutts 999 (NY).

### APPENDIX 2.

#### New infrageneric classification of *Gochnatia*.

##### KEY TO THE SECTIONS OF *GOCHNATIA*

1. Pappus type A (all bristles are thin and have the same length and width) and/or pappus type B (all bristles are thin and have the same width, but about half are shorter) ..... 2
- 1'. Pappus type C (all bristles are thin and have the same width, half of them are shorter, and the longer are plumose at the apex) or pappus type D (half of the bristles are long and wide, and the other half are short and thin) ..... 7
- 2(1). Subshrubs; capitula solitary, very long-pedunculate, or arranged in seapiform pseudocorymbs ..... *G. sect. Discoseris*

2'.	Trees or shrubs; capitula short-pedunculate or sessile	3
3(2).	Involucral phyllaries dorsally glabrous or subglabrous and ciliolate at the margins	4
3'.	Involucral phyllaries dorsally tomentose and not ciliolate at the margins	5
4(3).	Capitula arranged in glomerulose pseudocorymbs, pseudoracemes, or pseudopanicles; phyllaries extending into the peduncle	<i>G. sect. Leucomeris</i>
4'.	Solitary capitula; phyllaries not extending into the peduncle	<i>G. sect. Rotundifolia</i>
5(3).	Solitary capitula or 2 or 3	6
5'.	Capitula in glomerulose pseudocorymbs	<i>G. sect. Glomerata</i>
6(5).	Leaves spiny; corollas deeply to very deeply lobed	<i>G. sect. Anastraphioides</i>
6'.	Leaves not spiny; corollas deeply lobed	<i>G. sect. Gochnatia</i>
7(1).	Pappus type C; plants not glandulose, with 2-, and 3- to 5-armed hairs; gynomioecious or polygamous dioecious; corollas subdimorphic (isomorphic), 9–15(50)	<i>G. sect. Hedraiophyllum</i>
7'.	Pappus type D; plants glandulose; monoecious; corollas isomorphic, 5 (3, 7, or 10–20)	<i>G. sect. Pentaphorus</i>

***Gochnatia* sect. *Anastraphioides*** Jervis ex S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia ilicifolia* Less.

Arbores vel frutices, foliis alternis, spinoso-dentatis vel integerrimis. Capitula apicibus ramulorum, solitaria vel 2–3, sessilia. Involucrum campanulatum vel turbinatum. Flores 4–150, lutei vel aurantiaci, isomorphi, hermaphroditici, corolla tubulosa pentasecta vel profunde pentasecta. Antherae appendicibus connectivalibus caudatis vel abruptis, appendicibus basalibus integerrimis vel laciniatis. Pappus uniseriatus vel biseriatus.

Shrubs or small trees, monoecious. Leaves alternate, petiolate or shortly petiolate; obovate, oblong, or elliptic with margins spinose-dentate (rarely entire); pinnately veined; upper surface generally glabrous, lower surface densely tomentose (with flagellate hairs). Capitula homogamous, discoid, sessile, solitary at the tip of the branches (rarely 2 or 3). Involucrum campanulate or turbinate. Phyllaries in 4 to 10(15) series, dorsally tomentose. Flores 4 to 150, yellow or orange, hermaphroditic, isomorphic, tubulose, deeply to very deeply 5-lobed. Anthers with appendages caudate (rarely abruptly apiculate), and commonly smooth, occasionally laciniate tails. Style bilobate or shortly bifid; style branches rounded, dorsally glabrous. Cypelas with duplex hairs and commonly capitate glandular hairs (rarely with flagellate hairs). Pappus uniseriate with all bristles of the same length (rarely biseriate with a reduced number of outer short bristles) all thin.

Twenty-six species: *G. attenuata*, *G. buchii*, *G. calcicola*, *G. cowellii*, *G. crassifolia*, *G. cubensis*, *G. ekmanii*, *G. elliptica*, *G. enneantha*, *G. gomezii*, *G. ilicifolia* (type species), *G. intertexta*, *G. maisiana*, *G. mantuensis*, *G. microcephala*, *G. montana*, *G. obtusifolia*, *G. oligantha*, *G. parvifolia*, *G. pauciflosculosa*, *G. picardae*, *G. recurva*, *G. sagrana*, *G. shaferi*, *G. tortuensis*, *G. wilsonii*.

**Distribution.** Bahamas Islands, Cuba, Haiti, Dominican Republic, Puerto Rico.

**Observations.** As pointed out by Jervis (1954) and Ca-

brera (1971), *Anastraphia* D. Don (Trans. Linn. Soc. London 16: 295. 1830) is considered an unknown genus because its type (*Anastraphia ilicifolia* D. Don based on a "Joannes Fraser" specimen in the Lambert herbarium) has never been located. The original diagnosis of *Anastraphia* does not agree with the later interpretation of the genus by de Candolle (1838: 26).

***Gochnatia* sect. *Discosericis*** (Endlicher) Cabrera, Revista Mus. La Plata 12, Secc. Bot. 66: 150. 1971. *Seris* Less., non Willd. 1807, Linnaea 5: 253. 1830. *Seris* sect. *Discosericis* Endl., Gen. Pl.: 483. 1838. *Richterago* Kuntze, Rev. Gen. Pl. 1: 360. 1891. *Discosericis* (Endl.) T. Post & Kuntze, Lex. Gen. Phan.: 181. 1904, nom. superfl. TYPE: *Seris discoidea* Less. (= *Gochnatia discoidea* (Less.) Cabrera).

Subshrubs, monoecious. Leaves alternate, petiolate; ovate to ovate-elliptic with margins entire or denticulate; pinnately veined; glabrous or tomentose on both sides (with flagellate hairs). Capitula homogamous, discoid, long-pedunculate and solitary or arranged in scapose pseudocorymbs. Involucrum campanulate to turbinate. Phyllaries in 4 or 5 series, dorsally tomentose. Florets numerous (ca. 30), yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate and laciniate tails. Style shortly bifid; style branches rounded, dorsally glabrous. Cypselas with duplex and glandular hairs. Pappus uniseriate with all bristles of the same length and thin.

Three species: *G. amplexifolia*, *G. discoidea* (type species), *G. suffrutescens*.

*Distribution.* Southeastern Brazil.

***Gochnatia* sect. *Glomerata*** S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia arborescens* T. S. Brandegee (selected here).

Arbores vel frutices, foliis alternis, integerrimis. Capitula pauca, sessilia vel subsessilia, apicibus ramulorum glomerata. Involucrum campanulatum. Flores 12–50, lutei, isomorphi, hemaphroditici, corollis tubulosis, pentasectis. Antherae appendicibus connectivalibus attenuatis vel abruptis, appendicibus basalibus integerrimis. Pappus biseriatus vel uniseriatus.

Small trees or shrubs, monoecious. Leaves alternate, shortly petiolate; ovate to elliptic with margins entire or denticulate; pinnately veined; upper surface glabrous or tomentulose, lower surface usually densely tomentose (with flagellate hairs). Capitula homogamous, discoid, sessile or subsessile, few together in terminal glomerulose pseudocorymbs. Involucrum campanulate. Phyllaries in 5 or 6 series (rarely 8 to 10), dorsally tomentose or glabrous. Florets 12 to 20 (rarely ca. 50), yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate (rarely attenuate) and smooth tails. Style shortly bifid or bilobate; style branches rounded, dorsally glabrous. Cypselas with duplex and glandular hairs. Pappus biseriate of numerous scabrid bristles, with a reduced number of outer short bristles (rarely uniseriate with all bristles of the same length), all thin.

Three species: *G. arborescens* (type species), *G. magna*, *G. purpurea*.

*Distribution.* Northern Mexico.

***Gochnatia*** Kunth sect. ***Gochnatia***, Nov. Gen. Sp. 4: 15. 1818. TYPE: *Gochnatia vernonioides* Kunth.

Shrubs, monoecious. Leaves alternate, shortly petiolate; ovate or ovate-elliptic with margins entire (rarely denticulate); pinnately, occasionally subtri-veined; upper surface generally glabrous or tomentulose, lower surface densely tomentose (with flagellate hairs). Capitula homogamous, discoid, sessile or short-pedunculate, solitary (rarely 2 or 3). Involucrum oblong to campanulate. Phyllaries in 3 to 7 series, dorsally tomentose or only tomentose above. Florets 7 to 40, yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages caudate, more rarely abruptly apiculate, and laciniate tails. Style shortly bifid; style branches rounded, dorsally glabrous. Cypselas with duplex hairs and usually glandular hairs. Pappus biseriate of numerous scabrid bristles, with a reduced number of outer, short bristles, all thin.

Seven species: *G. arequipensis*, *G. boliviiana*, *G. cardenasi*, *G. curviflora*, *G. patazina*, *G. vargasii*, *G. vernonioides* (type species).

*Distribution.* Andes of Peru, Bolivia, and northwestern Argentina.

***Gochnatia* sect. *Hedraiphillum*** (Lessing) DC., Prodr. 7(1): 24. 1838. *Gochnatia* subg. *Hedraiphillum* Less., Syn. Gen. Compos.: 103. 1832. TYPE: *Gochnatia cordata* Less.

***Gochnatia* sect. *Moquiniastrum*** Cabrera, Revista Mus. La Plata 12, Secc. Bot. 66: 73. 1971. TYPE: *Spadonia polymorpha* Less. (= *G. polymorpha* (Less.) Cabrera).

Shrubs or trees, commonly gynodioecious or polygamous dioecious. Leaves alternate, petiolate or shortly petiolate; ovate, elliptic (rarely linear or cordate) with margins entire, rarely denticulate; pinnately veined; upper surface glabrous (rarely tomentose), lower surface densely tomentose (with 2-, 3- to 5-armed hairs, occasionally flagellate). Capitula heterogamous (homogamous), disciform (rarely discoid), subsessile to pedunculate, numerous arranged in terminal and usually loose leafy pseudopanicles. Involucrum oblong to campanulate. Phyllaries in 3 or 4 series, dorsally tomentose. Florets 9 to 15(50), creamy or white, tubulose, deeply 5-lobed, subdimorphic (occasionally isomorphic); functionally female, corollas slightly zygomorphic, with straight lobes; hermaphroditic, actinomorphic, with resupinate lobes. Anthers with appendages abruptly apiculate and laciniate or smooth tails. Style shortly bifid (rarely bilobate); style branches rounded, dorsally glabrous. Cypselas with duplex, glandular, and flagellate hairs. Pappus biseriate of numerous scabrid bristles, with a reduced number of outer short bristles, all thin, and the longest are plumose at the apex.

Twenty-one species: *G. argentina*, *G. argyrea*, *G. barrosii*, *G. blanchetiana*, *G. cordata* (type species), *G. densicephala*, *G. discolor*, *G. floribunda*, *G. gardneri*, *G. hatschbachii*, *G. haumaniana*, *G. mollissima*, *G. oligocephala*, *G. orbiculata*, *G. paniculata*, *G. polymorpha*, *G. pulchra*, *G. ramboi*, *G. rusbyana*, *G. sordida*, *G. velutina*.

*Distribution.* Andes of Peru and Bolivia, eastern Brazil, Paraguay, Uruguay, and central-eastern Argentina.

***Gochnatia* sect. *Leucomeris*** (D. Don) Cabrera, Revista Mus. La Plata 12, Secc. 66: 128. 1971. *Leucomeris* D. Don, Prodr. Fl. Nepal.: 169. 1825. *Gochnatia* subg. *Leucomeris* (D. Don) Less., Syn. Gen. Compos.: 103. 1832. TYPE: *Gochnatia spectabilis* (D. Don) Less. (= *Leucomeris spectabilis* D. Don).

*Trees or shrubs*, monoecious. *Leaves* alternate, shortly petiolate; elliptic, margins entire or denticulate; pinnately (3-)veined; upper surface generally glabrous to tomentose, lower surface densely tomentose (with flagellate hairs) or glabrous on both sides. *Capitula* homogamous, discoid, subsessile, many in glomerules, arranged in terminal leafy pseudoracemes, pseudopanicles, or pseudocorymbs. Involucre campanulate, oblong or turbinate. *Phyllaries* in 3 to 6(7) series, dorsally glabrous with ciliolate margins, extending to the peduncle. *Florets* 4 to 6 (8 to 12), white (rarely yellow), hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages attenuate (rarely abruptly apiculate) and lacinate tails (rarely smooth). Style bilobate or shortly bifid, style branches obtuse or rounded, dorsally glabrous. *Cypselas* with duplex hairs and commonly with glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer short bristles, all thin.

Five species: *G. hypoleuca*, *G. palosanto*, *G. smithii*, *G. decora*, *G. spectabilis* (type species).

*Distribution.* Mexico, Brazil, Andean region of Bolivia and Argentina, and southeastern Asia.

***Gochnatia* sect. *Pentaphorus*** (D. Don) DC., Prodr. 7(1): 24. 1838. *Pentaphorus* D. Don, Trans. Linn. Soc. London 16: 296. 1830. *Gochnatia* subg. *Pentaphorus* (D. Don) Hook. & Arn., Comp. Bot. Mag. 1: 108. 1835. TYPE: *Gochnatia foliolosa* D. Don ex Hook. & Arn.

*Shrubs*, monoecious. *Leaves* alternate, sessile; linear-ovate or linear-obovate with margins entire or upper portion denticulate; pinnately or three-veined; upper and lower surfaces glandulate (with or without flagellate hairs). *Capitula* homogamous, discoid, sessile or subsessile, numerous in leafy glomerulose pseudoracemes. Involucre campanulate. *Phyllaries* in 4 to 6 series, dorsally glabrous

or tomentulose with ciliolate margin. *Florets* 5 (rarely 3, 7, or 10 to 20), white or lilac, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate and smooth or lacinate tails. Style bilobate or shortly bifid; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* biseriate of numerous scabrid bristles, half of them relatively wide and long, and the others short and thin.

Two species: *G. foliolosa*, *G. glutinosa* (type species).

*Distribution.* Western Argentina and central Chile.

***Gochnatia* sect. *Rotundifolia*** S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia rotundifolia* Less. (selected here).

Frutices, foliis alternis, integerimis vel denticulatis. Capitula apicibus ramulorum solitaria, sessilia. Involucrum campanulatum; bracteis involucralibus subglabris, margine ciliatis. Flores multi, albi, isomorphi, hermaphroditici, corollis tubulosis, pentasectis. Antherae appendicibus connectivalibus attenuatis apiculatis, appendicibus basalibus laciniatis. Pappus biseriatus, setosus.

*Shrubs*, monoecious. *Leaves* alternate, shortly petiolate; broadly elliptic with margins entire to denticulate; three-veined, glabrous on both surfaces at maturity (young leaves with flagellate hairs). *Capitula* homogamous, discoid, sessile, solitary. Involucre campanulate. *Phyllaries* in 4 or 5 series, dorsally subglabrous with ciliolate margin. *Florets* ca. 50, white, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages attenuate and lacinate tails. Style bilobate; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer, short bristles, all thin.

One species: *G. rotundifolia*.

*Distribution.* Southeastern Brazil.